

# BIOLOGY AND EVOLUTION OF THE AVIAN GENUS ATLAPETES (EMBERIZINAE)\*

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ABSTRACT. The 24 species of *Atlapetes* are furtive brush or forest inhabitants occurring mainly in subtropical or temperate zones in the highlands from Mexico to the southern Andes. They are grouped into four subunits: (1) *A. albinucha* superspecies, (2) *A. rufinucha* species-group with *A. rufinucha* superspecies, *A. tricolor* superspecies, *A. albofrenatus*, *A. leucopis*, *A. pileatus*, *A. fulviceps* superspecies, and probably *A. citrinellus*, (3) *A. schistaceus* species-group with *A. schistaceus*, *A. nationi*, *A. leucopterus*, *A. albiceps*, *A. pallidiceps*, and *A. rufigenis*, and (4) *A. torquatus* species-group with *A. brunneinucha* and *A. torquatus* superspecies. The *A. rufinucha* species-group, with 11 (or 12) species, and the *A. schistaceus* species-group, with six species, are the main evolu-

tionary lines. Their respective members are largely allopatric, suggesting a recent origin. Speciation within *Atlapetes* seems to have been greatly influenced by Pleistocene climatic oscillations and to have been most active in the northern Andes.

## INTRODUCTION

Members of the genus *Atlapetes*, a moderately well-differentiated genus of emberizine sparrows, occur from the plateau of northern Mexico through the mountains of Central America and down the length of the Andes to northwestern Argentina (Fig. 1). There are 24 species, with the greatest number occurring in Colombia, where there are 14 species, and in Ecuador, where there are 11 species (Fig. 2). There is a general attenuation in the number of species north and south of the Colombia-Ecuador region. Several species have ranges that are restricted to a single valley system (*flaviceps*; *pallidiceps*) or massif (*melanocephalus*), while at the other extreme one species (*brunneimucha*) occurs from Mexico to Peru and has "a more extended range, . . . , than that of any other subtropical . . ." bird (Chapman, 1923a:245). However, for the most part, species of *Atlapetes* have ranges that are intermediate in length. The distribution of a number of species is discontinuous; at times the breaks appear to be unrelated to geography, vegetation, or collecting activities and offer clues to the evolutionary history of the genus.

All species are roughly the same size (ca. 130–180 mm long) and generally rather plainly marked. They are brown, brownish gray, or dark green dorsally and dull gray or bright yellow below. The majority have brown heads, the others are black with the exception of one which is white.

Members of the genus are characteristically furtive, seldom ascending more than a meter or two above the ground or emerging from the dense vegetation they

prefer. They are solitary during the breeding season but may assemble in what appear to be family groups at other seasons. While many brush-inhabitators have loud, easily recognized vocalizations, the calls and songs of members of the genus *Atlapetes* are faint and undistinctive. In some localities these birds seem to make up a substantial portion of the avifauna, but this is apparent only to the most diligent observer.

Considerable information is available on the distribution of the genus. This has provided material for my primary objective, which is to reconstruct the evolutionary history of the species of *Atlapetes*. The secondary purpose of this paper is to assemble what information is available on all aspects of this little-known group. Knowledge of the living birds is so scant that the best that can be done is to establish a foundation for future studies.

The arrangement of species in Peters' *Check-list* (Paynter, 1970:190–206) was based on a preliminary study of the genus. The present treatment is essentially the same, except that two taxa (*virenticeps* and *atricapillus*) that were treated as races of *A. torquatus* are now considered to be allopecies of the *torquatus* superspecies. I have also somewhat revised the sequence of species to reflect my present concept of their relationship.

Information on the distribution and habits of the genus has been gathered from published material, from a limited amount of my own fieldwork (principally in Mexico, Colombia, and Ecuador) and from the examination of museum specimens (mainly the rarer species or those with limited ranges). The occurrences of all 24 species have been plotted on the accompanying distribution maps. Without doubt some existing records have not been found, particularly among the many specimens of the common species, but additional data from collections should not materially alter

Figure 1. Distributional records for the genus *Atlapetes*.



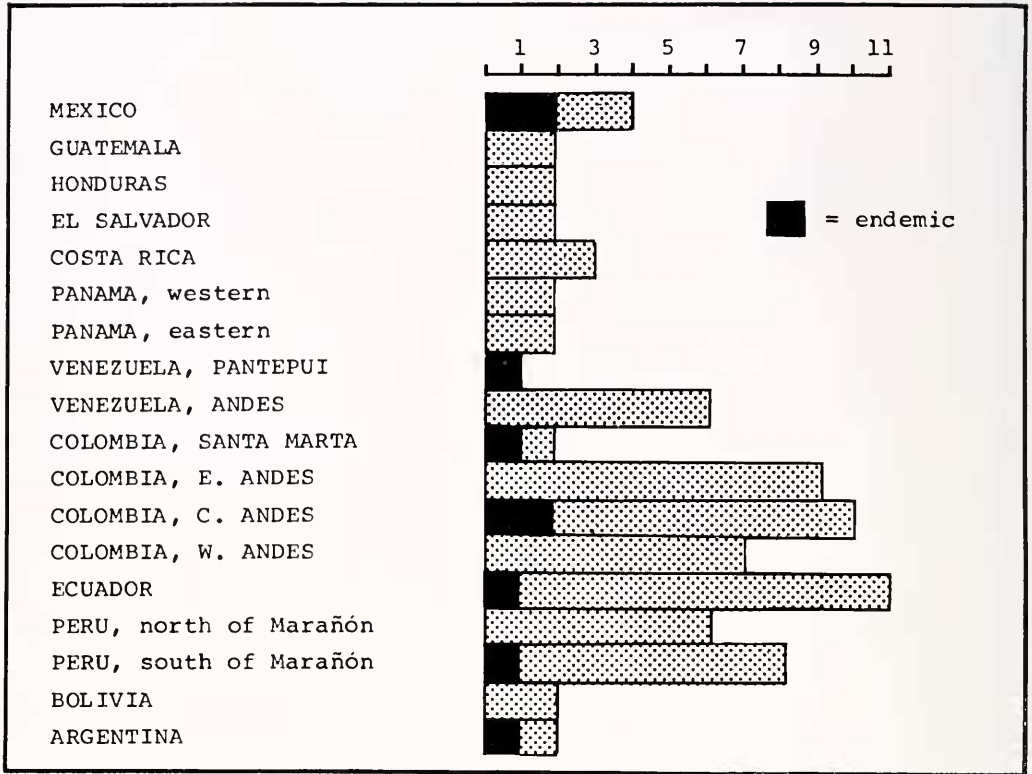


Figure 2. Geographical distribution of the 24 species of *Atlapetes*.

the depicted ranges of the more abundant forms. On the other hand, additional field-work should reveal more extensive ranges for at least some of the rarer species and for some of those whose distribution is now believed to be very restricted. Furthermore, one should not fail to appreciate that these maps show the distribution of each species from the time of its discovery until now. Therefore, the maps depict the maximum known ranges of the species. The enormous changes wrought on Neotropical vegetation during the past 100 years may have made the present-day ranges of some species more restricted than shown on the maps, while other forms may have flourished under these changes and occur outside the ranges as plotted.

To avoid repetition and cumbersome detail, I have not documented, by means of

literature citations or reference to museum specimens, every locality plotted on the distribution maps or mentioned in the text. The compilation of Hellmayr (1938:384-423) was the primary source; records from more recent publications and from museum material are on file and available to future workers.

The *A. schistaceus* species-group, containing *A. schistaceus*, *nationi*, *leucopterus*, *albiceps*, *pallidiceps*, and *rufigenis*, was analysed in an earlier paper (Paynter, 1972) and will not be treated in detail again.

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## DISTRIBUTION, HABITS, AND MORPHOLOGY

### *Atlapetes albinucha* superspecies

There are two allospecies in this superspecies, viz. *A. albinucha* and *A. pallidinucha*. Morphologically, they are only moderately similar, but it is their geographical and altitudinal distribution that leads me to believe that they share a common ancestor.

#### *Atlapetes albinucha*

*Range*.—*A. albinucha* is primarily a Middle American species of middle altitudes. It occurs from the Caribbean slope of central Mexico (Veracruz and Puebla), and the Pacific slope of southwestern Mexico (Chiapas), through the highlands of Central America to western Panama (Figs. 3, 4). It reappears in Colombia, where it occurs

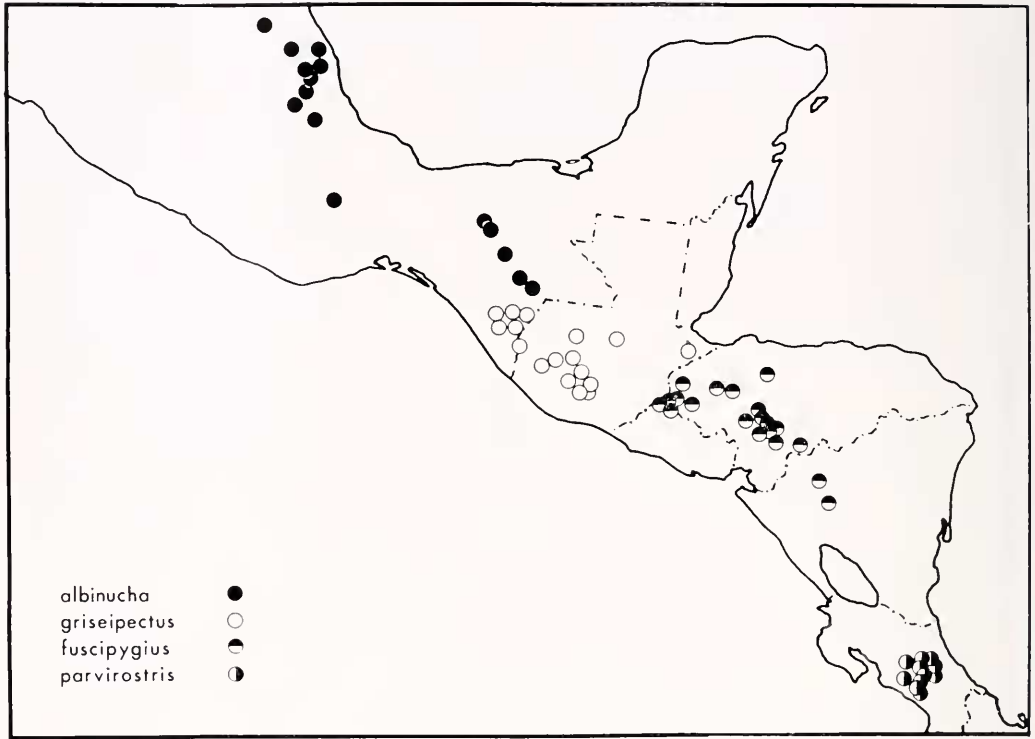
on all three ranges of the Andes except in the extreme south (Nariño) and in the Eastern Cordillera north of Cundinamarca.

This is a form principally of the humid subtropical and lower temperate zones. It has been found as low as 600 m in Mexico (Miller et al., 1957) and Costa Rica (Skutch, 1967) and up to 3,050 m in Guatemala (Land, 1970), but seems to occur most often from about 1,000 to 2,400 m. No latitudinal variation in altitudinal distribution is evident, in spite of Skutch's (1967) impression that the species occurs at higher elevations in southern Central America than in Mexico and Guatemala.

*Habitat*.—This atlapetes is found in thick vegetation near the edges of forests, in brushy woodland, and in dense second-growth, but not in the interior of heavy forest. It does not seem to occur regularly in pure stands of conifers, although Skutch (1967) once found it in low cypress. It is, however, common in mixed pine-broadleaf associations and in the low deciduous vegetation bordering pine forest (Dickey and van Rossem, 1938; Paynter, 1957; Skutch, 1967).

*Habits*.—*A. albinucha* is secretive and difficult to observe, as are all species of *Atlapetes*. Skutch (1967) reports that this species is even more shy than *A. brunneinucha* and *A. torquatus*. It generally occurs on or near the ground, but at times will go as high as 20 m (Slud, 1964); it roosts in trees (Skutch, 1967) and occasionally feeds there (Dickey and van Rossem, 1938; Skutch, 1967). Except when mated or accompanied by its young, the species is solitary (Skutch, 1967), sulking in the underbrush and seldom flying, and then only for short distances "in fluttering dips with [its] tail partially cocked" (Slud, 1964:282).

While in Honduras in April 1976, I saw this species for the first time in many years, and my attention was immediately drawn to the loud noise of the flapping wings, a characteristic I had first noticed in *A. nationi* (Paynter, 1972:303). One wonders whether the sound of the wingbeats, in-

Figure 3. Northern races of *A. albinucha*.

stead of voice signals, is a means of keeping members of a family group together, or whether the noise is merely an aerodynamic byproduct with no special significance.

Skutch (1967) saw the species feeding on berries of *Fuchsia arborescens*. This seems to be the only specific record of its diet but because the bird is often heard foraging in the forest litter, it may be assumed to be omnivorous. Skutch (1967) surmises that the bird turns the litter with its bill, although apparently no one has yet seen this behavior.

*A. albinucha* builds a bulky, open nest in weeds close to or on the ground or in dense tangles a meter or two above it (Cherrie, 1892; Blake, 1956; Skutch, 1967). Two or three white or pale blue eggs are laid, and at least some white eggs turn pale blue when their contents are removed (Cherrie, 1892). The nests are frequently parasitized

by *Molothrus aeneus* (Cherrie, 1892; Slud, 1964).

The breeding season is poorly known. In Middle America, it appears to be from April through June or even late July (Cherrie, 1892; Blake, 1958; Paynter, 1957; Skutch, 1967); in Colombia, March and April dates are recorded (Miller, 1963).

The call is said to be a faint high-pitched *tseep-tsee-cep* (Edwards, 1972) or *sst, sr*, or *tsr* (Slud, 1964), and its song is described as a weak "squeaky pully" sound with descending churrs (Slud, 1964) on a thin slow "O see me, O see, I'm weary, pity me" (Skutch, 1967).

*Morphological variation.*—There is minor sexual dimorphism in size, with the male's wing and tail averaging slightly longer and the bill minutely longer. No geographical variation in these characters is apparent.

There is very little variation in the color

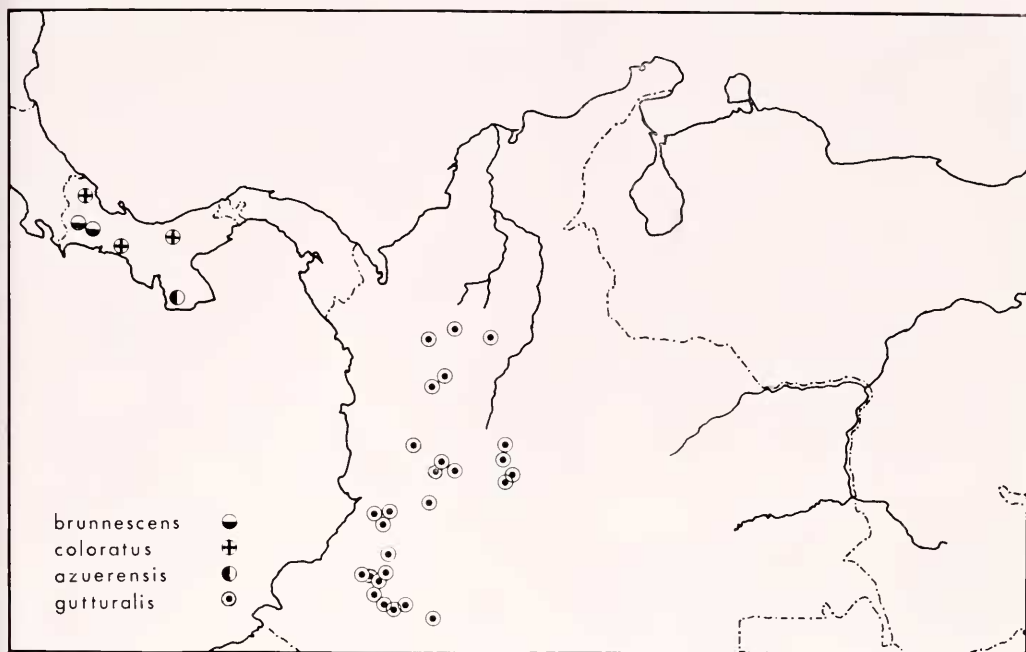


Figure 4. Southern races of *A. albinucha*.

of the populations from southernmost Mexico southward. The differences that do exist are clinal changes in the intensity of the yellow of the throat (and possibly in its extent), in the degree of brownish or blackish cast on the back, and in the grayness of the flanks. The variation in back color, however, may merely be a function of the age of museum skins. From southwestern Mexico to Colombia seven races have been recognized (Paynter, 1970) on the basis of color, but these are very weak races and at least two (*coloratus* and *azuerensis*) are almost certainly invalid. On the other hand, an eighth race, the population of eastern Mexico (nominate *albinucha*) is conspicuously different in that the entire underparts, rather than merely the throat, are yellow. There are no other differences.

*A. a. albinucha* was long treated as a distinct species. This is doubtless because it was originally described from Cartagena on the coast of Colombia (a most improbable locality for any form of *Atlapetes*),

and, consequently it was thought to occur only in Mexico and Colombia. Paynter (1964) pointed out that the collector of the holotype had visited both Colombia and eastern Mexico on the same voyage, and because there has never been another specimen of the taxon collected in Colombia, it is logical to assume the provenance of the type was wrongly recorded. The type locality was, therefore, amended to the Caribbean slope of Mexico, and Colombia was deleted from the range of *albinucha*.

*A. a. albinucha* does not intergrade with *A. a. griseipectus* of southwestern Mexico, Guatemala, and El Salvador, although the two forms are known to occur less than 100 kilometers apart in southwestern Chiapas. It is possible that the valley of the Río Grijalva (= Río Grande) is sufficiently low here to act as a barrier. The river is at approximately 1,000 m in this region while the bird has been taken on both sides of the valley at 1,500 m or higher. It could be

argued that since the two taxa are so nearly parapatric they should be treated as allospecies. Nevertheless, although the entirely yellow underparts of *A. a. albinucha* are conspicuously different from the gray abdomen and yellow throat of *A. a. griseipectus* and the remaining races, this dissimilarity almost certainly is not indicative of great genetic difference. Furthermore, it would appear that intergradation is prevented by a geographical barrier (low valley) and is not the result of ecological exclusion. I find it difficult to conceive that interbreeding would not occur if the taxa were in contact and believe that racial treatment of *A. a. albinucha* best reflects its status.

### *Atlapetes pallidinucha*

*Range*.—Occurs in the Eastern Andes of Colombia, barely extending into Venezuela, and through the Central Andes southward to central Ecuador (Fig. 5). In Ecuador this species seems to be almost absent on the western slope although there are many records from the eastern slope.

*A. pallidinucha* is principally a temperate region species, although on occasions it descends to the upper subtropical zone and ascends into the páramo zone. No other atlapetes is found in the páramo. It ranges from about 1,700 to 3,800 m, but most commonly from 2,000 to 3,100 m.

*Habitat*.—Olivares (1969) says the species is found in scrub and the remnants of forest. R. Webster (in litt.) noted the species sympatric with *A. rufinucha* in moist shrubbery and in forest edges in Ecuador. It is also sympatric with *A. torquatus* in similar habitats around Bogotá (Webster, in litt.; Donahue, verb. comm.).

*Habits*.—Although Olivares (1969) found *A. pallidinucha* to be the most abundant "fringillid" in Cundinamarca, and the number of records from elsewhere also suggest it is a common species, nothing seems to have been recorded of its habits or voice.

*Morphological variation*.—Females have slightly shorter wings and tails than the males.

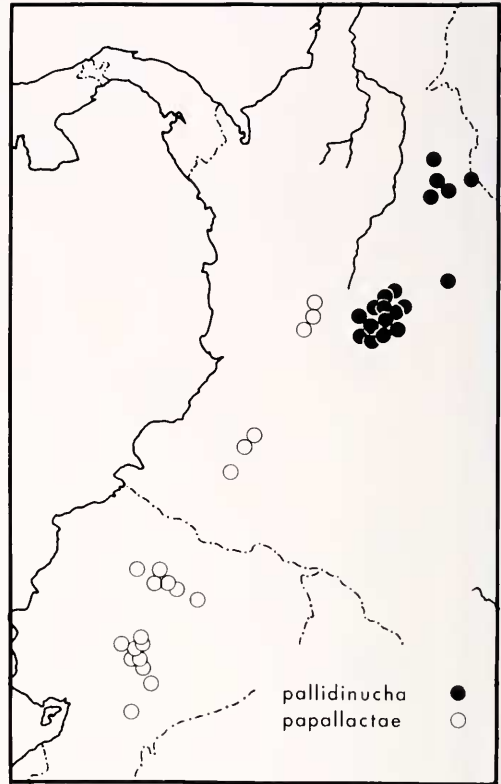


Figure 5. Distribution of *A. pallidinucha*.

Two races are recognized, the nominate form from the Eastern Cordillera of Colombia and adjacent Venezuela, and *A. p. papallactae*, a somewhat darker race, from the remainder of the range.

### *Atlapetes rufinucha superspecies*

*A. melanocephalus*, which is endemic to the Sierra Nevada de Santa Marta, Colombia, seems to have been derived recently from nearby *A. rufinucha*. The two taxa are, therefore, treated as allospecies.

### *Atlapetes rufinucha*

*Range*.—*A. rufinucha* has a wide but disjunct distribution in the Andes (Figs. 6, 7). It reaches its northernmost point in the

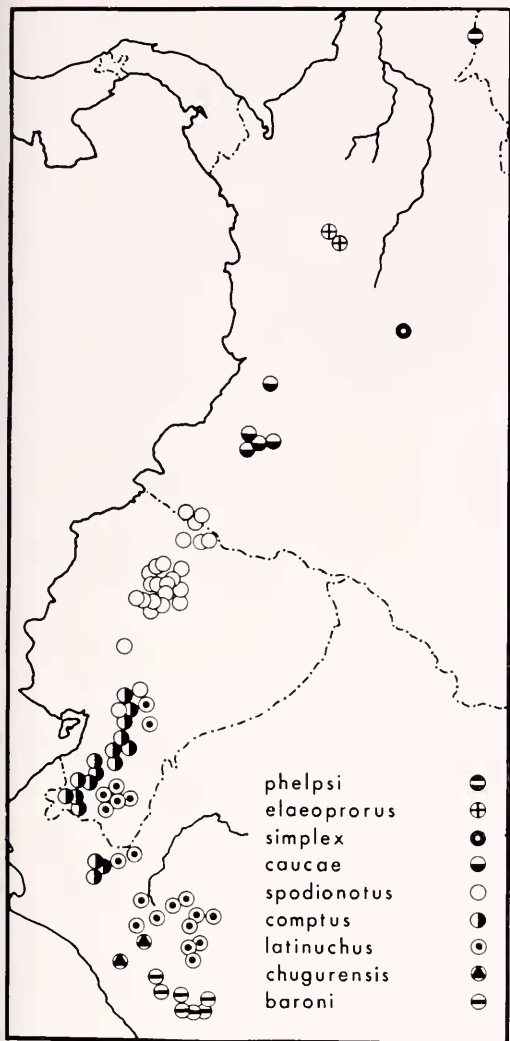


Figure 6. Northern races of *A. rufinucha*. *A. r. simplex* is recorded from "Bogotá" but probably comes from farther south in the Eastern Andes.

Sierra de Perijá along the Colombia-Venezuela border (*A. r. phelpsi*). It next occurs in three widely separated localities in central Colombia, viz., near the northern end of the Central Andes (*A. r. elaeoprorus*), possibly in the central or southern portion of the Eastern Cordillera although it is known only from native "Bogotá" specimens (*A. r. simplex*), and in south-central Co-

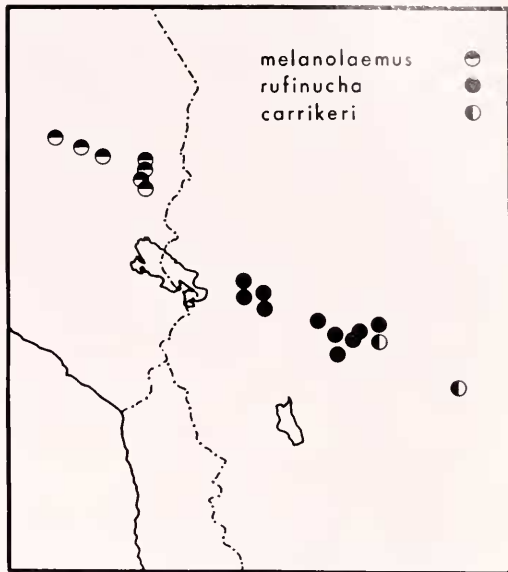


Figure 7. Southern races of *A. rufinucha*.

lombia on the western slope of the Central Andes and on the eastern slope of the Western Andes (*A. r. caucae*).

The species then occurs, more or less continuously, from Nariño, southern Colombia, south on the Pacific slope and interandean plateau through Ecuador to northwestern Peru (*A. r. spodionotus* south to central Ecuador where it intergrades with *A. r. comptus* of farther south). On the Amazonian slope of Ecuador there are records from the north in the vicinity of Papallata, but for the next 250 kilometers the species is absent; it reappears in Azuay, as the race *latinuchus*, and is common from here southward well into Peru. It is almost certain that the distributional gap is real and not a collecting artifact; several areas within the gap have been well-collected (see Paynter and Traylor, 1977:138).

In northern Peru *A. r. comptus* occurs on the western slope in Piura and is replaced farther south by *A. r. chugurensis*. On the eastern slope *A. r. latinuchus* reaches Amazonas and *A. r. baroni* is in southern Cajamarca and Libertad, just entering the Pacific drainage west of the upper reaches of



the tributaries of the Marañón west of Cajamarca. The species is found no farther south on the western slope but recurs on the Amazonian slope in southern Peru (Fig. 7) in Cuzco and Puno (*A. r. melanolaemus*) continuing through eastern Bolivia (nominate *rufinucha*) to Santa Cruz (*A. r. carrikeri*). While the gap in distribution in eastern Ecuador seems genuine, the gap in eastern Peru is less certain, owing to the paucity of collections from that region.

It is a species of subtropical and, less often, temperate regions. It has a notably wide altitudinal distribution, ranging from as low as 600 m in Bolivia (nominate *rufinucha*; range 600–3,350 m) to as high as 3,700 m in southernmost Colombia (*A. r. spodiionotus*; range 1,760–3,700 m). While there seems to be a tendency for the species to occur at generally higher elevations near the equator, the data are too scanty to confirm this. It is probable that the equatorial population will be found to average only a few hundred meters higher than those populations at the ends of the range.

*Habitat*.—Mainly in thick mesophytic scrub of moderate height, but also found in drier or wetter situations. It seems to be most common in moderately wet habitats, although near Gonzanamá, Loja, in southern Ecuador, I once observed it in small numbers in a rather dry subtropical area which was also occupied by *A. nationi simonsi* (Paynter, 1972:303) and there are numerous records of the species in the dry interandean region of northern Ecuador.

*Habits*.—I observed the species on several occasions in southern Ecuador and noted it to be somewhat less shy and more arboreal than most species of *Atlapetes*. At each observation, the species was from half a meter above the ground to as high as six meters. In the latter instance a small flock was feeding in bromeliads and other epiphytes. The species is notably active for an *atlapetes*. It moves about in flocks of up to five or six individuals, at least when not breeding. These observations confirm those of Taczanowski (1884) made in Peru.

Little is known of the breeding season. No breeding was noted in a long series of specimens collected from late July through October in southern Ecuador (MCZ collection). Chapman (1927) reported a male with much enlarged testes in Cajamarca, Peru on 20 April.

I have heard *A. rufinucha* give two calls. One is a single high-pitched thin *æep*, which seems feeble for a bird of its size. This call appears to be given when a bird is concealed and relatively inactive. Presumably it is used to communicate with other members of the flock when they are scattered and out of sight. The second call is a series of louder, lower-pitched notes resembling the calls of squabbling flycatchers, such as *Myiozetetes similis*, although not nearly so loud. This call has been heard when a flock is actively moving about; several birds may call at once. No song has yet been noted.

*Morphological variation*.—Twelve races have been described. Most of them are extremely well-differentiated from one another. *A. rufinucha* is, morphologically, one of the most variable species within the genus, even exceeding highly variable *A. torquatus*.

No clear difference in size is evident between the various subspecies although the few measurements that are available for the southernmost race (*A. r. carrikeri*) suggest that its wing and tail may be slightly shorter than those of other subspecies. In contrast to size, however, some of the variations in color are striking.

In addition to more subtle or gradual differences in the color of the tail, venter, etc., there are six characters that vary markedly within the species (Table I). No pattern of variation of a single character or correlation of one character with another appears to exist. For example, a sizable alar speculum is present in *elaeoprorus*, *cauceae*, and *latinuchus*, but all three forms are widely separated from one another and not bridged by either *chugurensis* or *simplex*, the two forms with small (or inconsistently present)

TABLE 1. MAJOR MORPHOLOGICAL VARIATIONS IN *A. rufinucha*.

	Alar speculum	Yellow loral spot	Throat pattern	Forehead	Crown	Back
<i>phalpsi</i>	lacking	lacking	chin black, broad malar streaks	broad black	chestnut	gray; slight olivaceous tinge
<i>elacopterus</i>	large	small	faint malar streaks	as crown	chestnut	gray; strong olivaceous tinge
<i>simplex</i>	lacking or small	small to very small	faint malar streaks	as crown	dark chestnut	gray; oliva- ceous tinge
<i>caucae</i>	large	small	faint malar streaks	as crown	dark chestnut	slate
<i>spodionotus</i>	lacking	lacking	moderate malar streaks	as crown	chestnut	very dark gray
<i>comptus</i>	lacking	large	large malar streaks	as crown	rufous	dark gray
<i>latinuchus</i>	medium	lacking or very small	very faint malar streaks	as crown	chestnut	very dark slate
<i>chungurensis</i>	small	small	very faint malar streaks	as crown	light chest- nut; paler on nape	dark slate
<i>baroni</i>	lacking	large	moderate malar streaks	as crown but with encroaching yellow	rufous; very pale nape	dark gray
<i>melanolacmus</i>	lacking	lacking	nearly all black	narrow black	chestnut	black
<i>rufinucha</i>	lacking	large	moderate malar streaks	narrow black	chestnut	black
<i>carrikeri</i>	lacking	lacking	moderate malar streaks	narrow black	chestnut	dark gray; olivaceous tinge

patches. Another example is the yellow loreal spot that is present in *elaeoprortus*, *simplex*, *caucaea*, *comptus*, *chugurensis*, *baroni*, and nominate *rufinucha*, all of which, with exception of *chugurensis* and *baroni*, are well separated from one another, either by distributional gaps or by the presence of taxa lacking the character. Even *melanolaemus* and *carrikeri*, which resemble one another more than they do any other races are not contiguous or even proximate, but are separated by nominate *rufinucha* which is more similar to the northern races.

Noteworthy, because it might appear to be a clue to evolutionary relationships, is the fact that *A. r. baroni* bears a very strong resemblance to *A. pallidinucha papallacta*. However, I do not think the two are related. The latter is larger and greener, ventrally, with the white of the nape more restricted, and its white feathers edged with black.

#### *Atlapetes melanocephalus*

*Range*.—Endemic to the Sierra Nevada de Santa Marta, Colombia (Fig. 8) where it occurs in the upper tropical and the subtropical zones at altitudes from 600 to 2,400 m.

*Habitat*.—Reported by Todd and Carriker (1922:525) to occur in "almost all kinds of conditions throughout its range—in the forest, scrub-growth, and even in low bushes in the open."

*Habits*.—In contrast to other members of the genus, *A. melanocephalus* is stated by Todd and Carriker (1922:525) to be "not at all shy"; they also note that it keeps near to the ground, moves about in pairs, and lays two white eggs in a domed nest low in a bush. No other atlapetes is yet known to build a domed nest and for that reason the observation is suspect.

#### *Atlapetes tricolor superspecies*

The three species comprising this super-species are little-known but they are, morphologically, quite similar, except for the

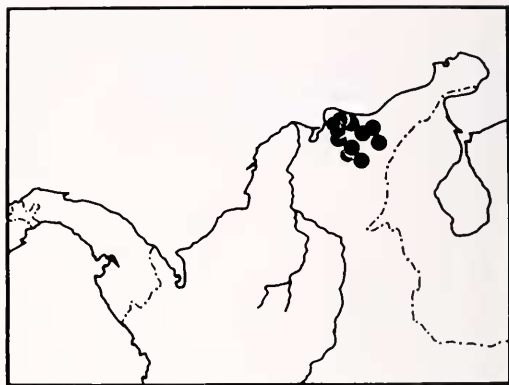


Figure 8. Distribution of *A. melanocephalus*.

color of the pileum. I have no hesitancy in postulating a monophyletic origin for them.

#### *Atlapetes flaviceps*

*Range*.—Known from only two specimens collected over 65 years ago in the subtropical zone (2,050–2,160 m) at Toche and Río Toche in a deep valley on the Nevada de Tolima on the eastern slope of the Central Andes of Tolima, north-central Colombia (Fig. 9).

*Habits*.—Nothing is known of the living bird.

#### *Atlapetes fuscolivaceus*

*Range*.—Most of the few known specimens were collected at least 50 years ago. These specimens and more recent observations indicate that the species occurs only in the subtropical zone, at altitudes from 1,500 to 2,400 m on the eastern side of the Central Andes in the upper Magdalena Valley, Huila, Colombia (Fig. 9).

*Habitat*.—The four localities from which the species is known (San Agustín, La Palma, La Candela, and Moscopán) are (were?) in the region of dense, tall, subtropical forest. I have seen one specimen bearing on its label the notation "forest."

Between 3–5 April 1977, I saw the species three times at San Agustín. I observed one bird in very thick, 2-meter high second-

growth; the second was in a hedgerow with dense brush and small trees up to 5 meters in height, and the third was in a row of 15-meter trees whose tops were only slightly above the level of a road cut into the side of the hill. Although in a region of high rainfall, the sites where the birds were noted were not particularly lush. There remain patches of fairly high forest around the archaeological sites of San Agustín, but no atlapetes were seen within the forest.

*Habits*.—Only single birds were seen at San Agustín. No calls were given, but once the beat of the wings, a characteristic noted in several other forms of *Atlapetes*, was heard as the bird flew off.

Two of the three birds seen were surprisingly high in the vegetation. One was two meters above the ground and easily seen against the horizon, but it quickly dropped down when approached. The other was in the crown of a 15-meter tree, where it was leisurely feeding on dark purple or black fruit about 5 mm in diameter in company with various tanagers, warblers, and a Swainson's thrush (*Catharus ustulatus*). The bird was watched for five minutes until it dropped down into shrubs and disappeared. The rich yellow underparts, and even the streaked throats, were conspicuous on these two birds whose behavior was in such contrast to the usual furtive demeanor of other atlapetes.

Chapman (1914) reported the type specimen, a male from San Agustín, had much enlarged gonads. The specimen probably was collected in April or May (see Chapman, 1917:45).

### *Atlapetes tricolor*

*Range*.—The species is known in Colombia on the eastern slope of the Western Andes from a single specimen (San Antonio, Valle) and on the western slope of the same range from several specimens taken from Caldas south to Nariño, with the majority of reports from the latter department. Although San Antonio is the type locality for the species (specimen taken by

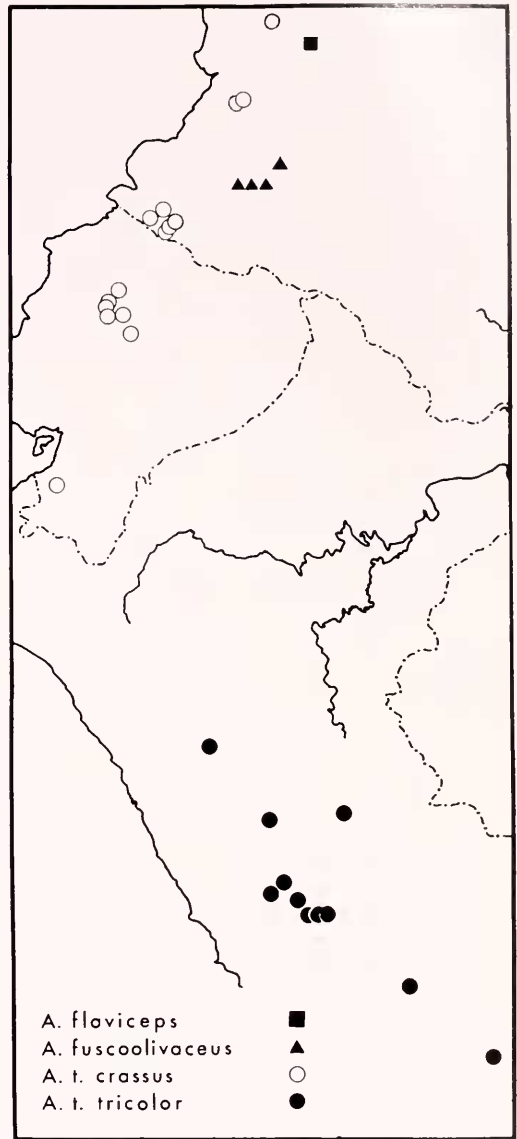


Figure 9. Distribution of *A. tricolor* superspecies.

M. G. Palmer, 11 Dec. 1907, according to Bangs, 1908:61), the absence of any other record from the eastern slope of the Western Andes makes the record suspect. Furthermore, in a year spent at San Antonio in 1958–59, Miller (1963) failed to find this species. There is a cluster of records from



adjacent northwestern Ecuador and a single specimen, far to the south, from La Chonta, El Oro, in southwestern Ecuador, again on the western slope. The species is absent in northern Peru but reappears in central Peru on the eastern slope in San Martín and ranges south to Cuzco (Fig. 9).

The species seems to have a particularly wide altitudinal range in the northern portion of its distribution, occurring from somewhat below 300 m up to 2,000 m and from the moist upper tropical zone to the subtropics. In Peru, however, it seems not to occur much below 1,700 m and ranges up to at least 2,400 m which means that in this region it is a species of the subtropical and lower temperate zones.

*Habitat*.—Taczanowski (1884) quoted Jelski's observation that the bird frequented dense thickets. Terborgh (in litt.) has seen it in Peru in elfin forest which was barely shoulder high and in undergrowth bordering small clearings. R. Webster (in litt.) saw the species around Tandapi [= Manuel Comejo Astorga; 00°25'S/78°48'W], Ecuador in dense thickets within the forest and on its edges.

*Habits*.—This atlapetes seems to be rare. It is little-known; Jelski observed it in Peru nearly a century ago (Taczanowski, 1884) and reported it to be a shy bird that moves about in small bands, but becomes more bold and more visible when courtship and song begin in February.

Richard Webster (in litt.) saw the species in June and September 1975 at three places on the slopes between Tandapi and above Santo Domingo de los Colorados, Ecuador. On 19 June at Tandapi he saw three pairs in an hour and a half; one pair was feeding a fledgling. Webster describes the species as being noisy, with a call of "a squeak followed by two chirps," many single squeaks, and a song of "sweet [slight pause], churr." In early September, he noted the species in a mixed flock of *Synallaxis azara*, *Myiodynastes miniat* and *M. chrysocephalus*, *Pipraeidea melanonota*, and *Tangara nigroviridis*. Jelski (Taczanowski, 1884) re-

ported that flocks of *A. tricolor* are sometimes accompanied by one or two individuals of *A. schistaceus*.

*Morphological variation*.—The northern and southern populations, which are widely separated, have been recognized as racially distinct. The northern race (*crassus*) has a noticeably thicker and longer bill and is generally darker and more richly colored.

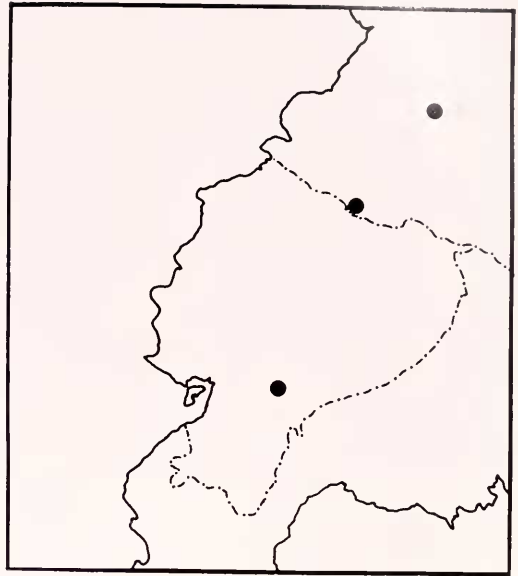
de Schauensee (1951) thought that there might be sufficient variation in the northern taxon to warrant naming additional races. This led Miller (1960) to believe *crassus* might even be a distinct species, but de Schauensee had based his speculations on the mistaken belief that the type of *crassus* has a brown crown, when it is instead merely a rich, tawny gold, not differing appreciably from other specimens from Colombia and Ecuador.

#### ***Atlapetes albofrenatus***

*Range*.—Occurs in the Eastern Andes of Colombia from about Bogotá northward to Santander and in the Andes of Venezuela in Táchira and Mérida (Fig. 10). Its altitudinal range is from about 1,000 to 2,500 m, but it seems mainly to occur above 1,600 m, and thus most often inhabits the subtropical zone and less frequently the upper tropical zone.

*Habitat*.—I saw the species on two occasions, 1–2 April 1975, in thick subtropical cloud forest, as well as in more open scrub, a short distance north of Bucaramanga, Colombia, at altitudes of 2,000–2,400 m. The birds moved into somewhat exposed situations for brief periods but preferred dense tangles such as the masses of ferns and bamboo that cascade over road cuts. Phelps and Phelps, Jr. (1963) imply that in Venezuela it is a species of forests. Webster (in litt.) informs me that he saw this atlapetes at altitudes ranging from 2,100 to 2,300 m, in dry, thorny, low scrub, on the mountains above Villa de Leiva, Boyacá, Colombia. The species' tolerance of a wide range of vegetation is confirmed by Olivares who wrote (in litt.) that the bird "occurs in low



Figure 10. Distribution of *A. albofrenatus*.Figure 11. Distribution of *A. leucopsis*.

forest which ranges from dry to moist, as well as in very humid subtropical forest."

**Habits.**—North of Bucaramanga the species was seen singly, paired, and in what appeared to be small family groups. They were mainly close to the ground but at times 10 m high in trees. In general their movements were, conspicuously, more rapid than those of *A. schistaceus*, which was also noted in the same area. The only call heard was a thin "zeep," characteristic of the genus. Webster (in litt.) also noted the species' propensity to range high in trees in the scrubby oaks bordering streams on the dry slopes above Villa de Leiva. Olivares (in litt.) has found the species in the lower branches of trees in the interior of the forest and says that an examination of several stomachs revealed mainly insects in some, while others contained more seeds. I observed a bird catch a small white moth.

**Morphological variation.**—Two well-differentiated races are recognized. The race *meridae*, of the Mérida Andes, which is separated from nominate *albofrenatus* of the Eastern Andes of northern Colombia by

the valley of the Río Torbes, is markedly different in having reduced malar stripes, a forehead that is concolor with the crown instead of being black, and underparts that are entirely yellow rather than white on the throat and upper breast. No difference in size is apparent.

### ***Atlapetes leucopsis***

**Range.**—Known with certainty from only three localities, apparently all in the subtropical zone (Fig. 11). The first is at La Plata (2,350 m) which is in a deep valley on the eastern slope at the southern end of the Central Andes and at the head of the Magdalena Valley in Huila, Colombia. The second is on Cerro Pax (alt. ?), which is on the eastern slope in Nariño, also in southern Colombia. The third is at Palmas (ca. 2,500 m), Azuay, on the eastern slope of southeastern Ecuador. The species was described from "Yauayaca" [= ? Yanayacu, *vide* Paynter and Traylor, 1977], a locality somewhere on the east slope of Ecuador.

**Habitat.**—Unknown.

**Habits.**—Only eight specimens are be-

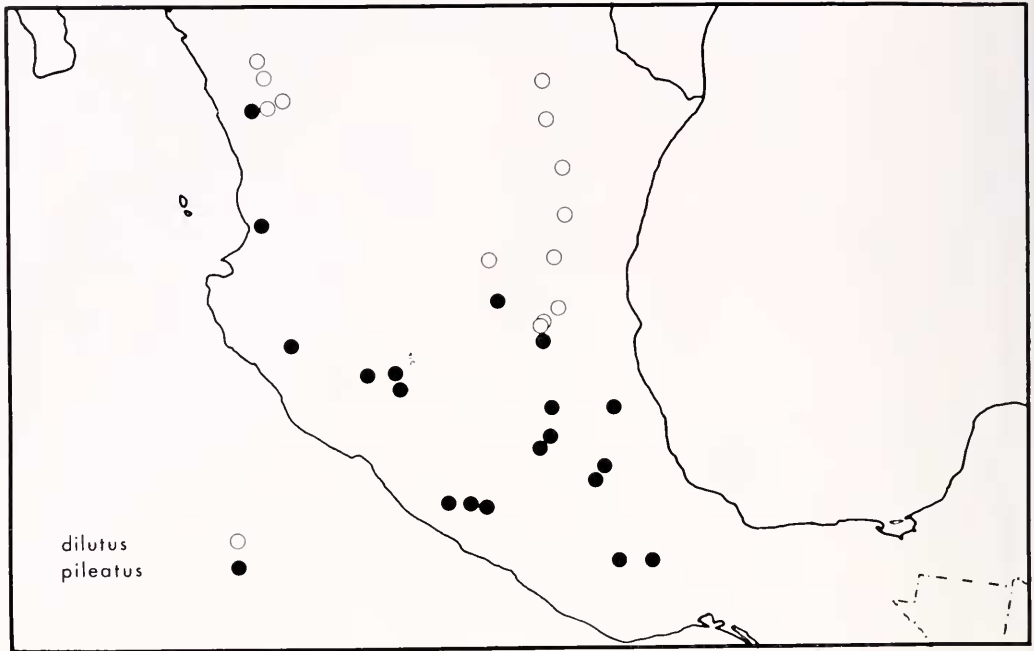


Figure 12. Distribution of *A. pileatus*.

lieved to exist (de Schauensee, 1951). It is among the least known of all atlapetes. There are no accounts of the living bird.

*Morphological variation.*—de Schauensee (1951) noted that a single bird from La Plata differed in color from four specimens from Cerro Pax, but there is no way to appraise the significance of this single observation.

### *Atlapetes pileatus*

*Range.*—Distributed on the Mexican Plateau from Chihuahua and Tamaulipas south to Oaxaca (Fig. 12). Occurs from 900 to 3,500 m, but most commonly from 1,500 to 2,800 m, in the temperate zone.

*Habitat.*—Moderately moist undergrowth, usually at edges of pine, oak, or pine-oak forest.

*Habits.*—Little is known of the habits of this secretive bird, which does not seem to be particularly common anywhere.

It has been described as remaining within

a few feet of the ground, moving rapidly, being "nervous," and jerking its tail (Edwards, 1972). Cody and Brown (1970) report that 90 percent of the bird's foraging is done on the outer branches of small trees and bushes and that, at least during the breeding season in Oaxaca (late March–early April), the species seems to be insectivorous. There is no further information on feeding habits.

The breeding season is prolonged, extending from late April in Oaxaca (Cody and Brown, 1970) to the end of August in San Luis Potosí (Miller et al., 1957).

The voice, which is "thin" and delicate, has been described by Edwards (1972:257) as "a high-pitched *wees*, a metallic *chip*, a *chip-chip-chip* chatter; and several song variations of a series of notes, such as *chip-ee-wee-wee-wee* or *chip-ee-r-r-r-r-r-r*, ascending in pitch to the first *wee* or *r-r* note."

*Morphological variation.*—The northern population (*A. p. dilutus*) is slightly smaller and generally paler than the nominate form.

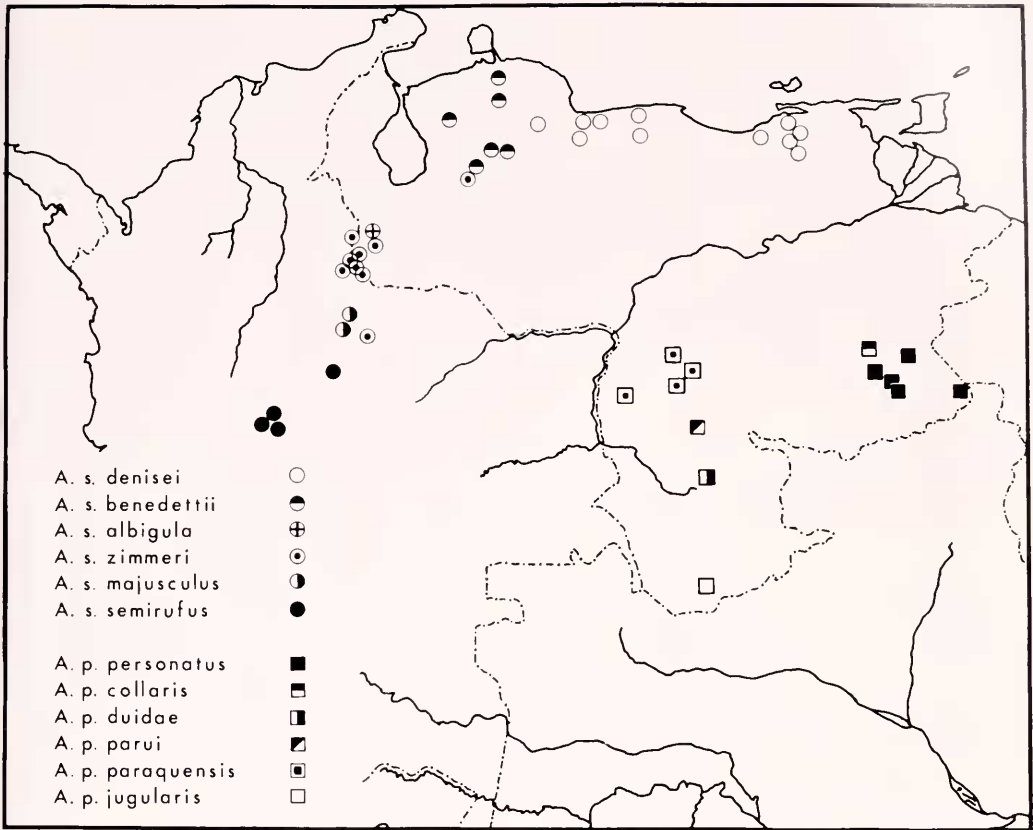


Figure 13. Distribution of *A. semirufus* and *A. personatus*.

These differences are easily distinguished but of no great magnitude. It is noteworthy that this is one of the few atlapetes exhibiting intraspecific variation in size.

#### *Atlapetes fulviceps* superspecies

This superspecies consists of three allopecies, viz. *semirufus*, *personatus*, and *fulviceps*. Although widely separated geographically (Figs. 13, 14), the three are morphologically very similar, with chestnut heads, yellow underparts, and green backs. Chapman, as long ago as 1931, postulated that *personatus* and *fulviceps* might be conspecific; this may be the eventual disposition of all three taxa, but I should like to

know more of the living birds before taking this step.

#### *Atlapetes semirufus*

*Range*.—Occurs from the coastal cordillera of northern Venezuela southward through the mountains to Cundinamarca in the Eastern Andes of Colombia (Fig. 13). At the northeastern extremity of its range the species (*A. s. denisei*) descends to as low as 600 m in the upper tropical zone and ascends as high as 2,100 m in the subtropical zone. Elsewhere the species does not occur below 1,200 m and is in the subtropical zone, exclusively, except at its southernmost limits where in the vicinity of Choachi,

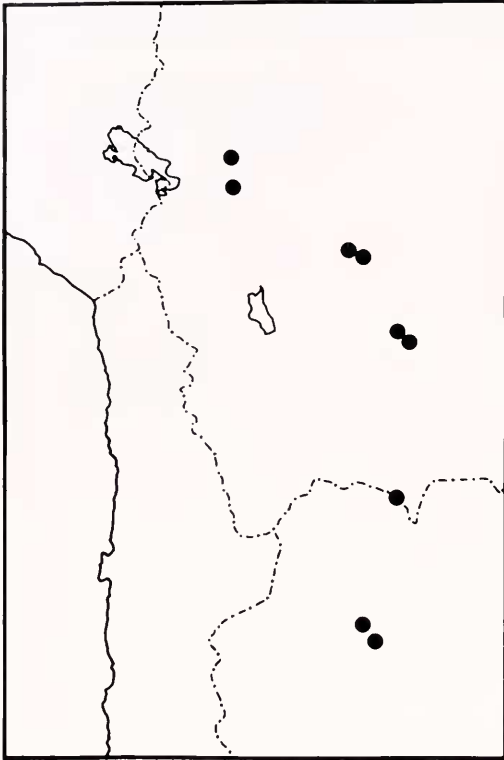


Figure 14. Distribution of *A. fulviceps*.

Cundinamarca it ranges between 3,000 and 3,500 m and is in the temperate/subpáramo zone (Olivares, 1969).

*Habitat*.—Schäfer and Phelps (1954) reported that *A. s. denisei* has a wide ecological range, occurring in moderately moist to somewhat xerophytic second-growth and in the weeds of low forest. Nothing seems to have been published concerning the habitat requirements of the other races. Because they appear to be confined to the subtropical zone (or temperate zone in the case of nominate *semirufus*), they probably have more restricted habitat preferences.

*Habits*.—Again, all we know about this species is contained in the brief account by Schäfer and Phelps (1954). They found that at Rancho Grande, Aragua, Venezuela the bird is of limited abundance, sedentary, and occurs in pairs or in groups of up to

eight individuals. Breeding is from May to July.

Schäfer and Phelps' observations suggest that this species might benefit by the creation of second-growth through human activity; one might even imagine the bird becoming more abundant than it was in the past. However, Olivares (1969) observes that in Cundinamarca, it was common early in this century, and he implies that thereafter it was exceedingly rare until a number of birds were discovered at Une in 1967. Whether this is an indication of a recovery of the species as a whole or merely the fortuitous discovery of a restricted population is unknown.

*Morphological variation*.—Morphological variation is not great, although six races have been recognized. Geographical variation in the shade of green on the back and of the brownish rufous and yellow on the venter are the obvious differences. There may be variations in size, but if so, they are of no great magnitude as they are not detectable in the limited material available for study.

### *Atlapetes personatus*

*Range*.—Found in scattered and isolated populations in the moist subtropical zone, between 1,000 and 2,500 m, on the table mountains ("tepuis") of southern Venezuela and adjacent Brazil (Fig. 13).

*Habitat*.—From the descriptions of Chapman (1931) it appears that the species occurs in the brushy wet forests on the summits of the tepuis.

*Habits*.—Nothing recorded.

*Morphological variation*.—The species has been divided into six subspecies, most of which are well-differentiated by color, pattern, or both. There are two basic color patterns, viz., that in which the bird's entire head, chin, throat, and chest are chestnut and that in which the chestnut does not extend to the throat and chest. Nominate *personatus* and *A. p. collaris* occur in southwestern Bolívar in relatively close proximity. They are of the latter type and the re-

maining four races, which lie to the west, have the former pattern. The two color patterns correspond to the two zoogeographical subdivisions of the "pantepui" region which lie on either side of the Río Caura (Mayr and Phelps, 1967). Variation within these two groupings is in the extent of the chestnut color or in the general intensity or shade of the colors. No significant differences in size have been noted.

### *Atlapetes fulviceps*

**Range.**—This little-known species has been recorded from the eastern slopes of Bolivia (La Paz to Chuquisaca) and in northwestern Argentina, apparently from about 400 m to as high as 2,700 m (Fig. 14). Hellmayr (1938) states that this is a form of the subtropical zone, but if the altitudinal range is as wide as the collecting records seem to indicate, the species must reach the temperate, or at least subtemperate, zone. Apparently this is a very rare bird in Argentina.

**Habitat and habits.**—Nothing recorded.

**Morphological variation.**—No geographical variation in morphology has been detected.

### *Atlapetes citrinellus*

**Range.**—The species, which is the southernmost representative of the genus, is restricted to the subtropical slopes of the Andes in Salta, Jujuy, and Tucumán, northwestern Argentina, from about 1,000 to 3,100 m (Fig. 15). I can find no substantiation for Olog's (1963) inclusion of Catamarca within the range. There is one suspect record from northern Paraguay (Bertoni, 1924).

**Habitat.**—Dinelli (1918) reported that the species occurs in dense ferns in shady, humid ravines; Wetmore (1926) found it in thick weeds at the edge of a grove.

**Habits.**—Dinelli (1918) noted this bird on the ground in small groups and reported it is not timid and is readily lured into sight when its call is imitated (described as a faint "tsip" by Wetmore, 1926). This is a

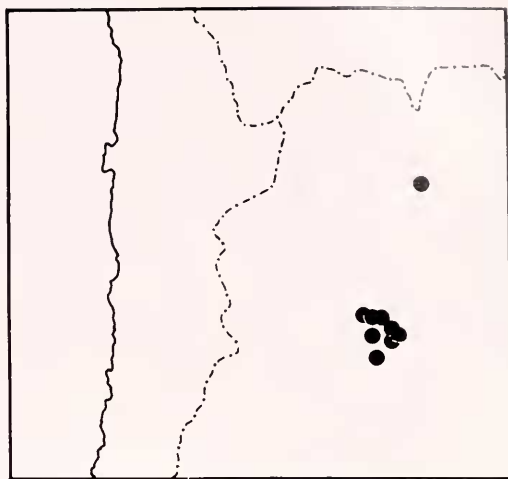


Figure 15. Distribution of *A. citrinellus*.

remarkably different type of behavior for an atlapetes. Dinelli (1918) describes the nest as being about 1½ m above the ground in a shrub. The egg is rosy-pink or white with dark brown or maroon spots and blotches, principally at the large end (Dinelli, 1918; Smyth, 1928). Smyth (1928) implies that a clutch consists of three eggs, and Pereyra (1951) also mentions a nest with three eggs; the latter was collected on 21 November, which is the only breeding date available for this little-known bird. Unfortunately, there appears to be no description of the nest itself.

**Morphological variation.**—There is no indication of either sexual or geographical differences in morphology.

### *Atlapetes brunneinucha*

**Range.**—*A. brunneinucha* ranges from northwestern Mexico to southeastern Peru (Figs. 16, 17) and thus has the most extensive distribution of any atlapetes. It is a species of humid regions, generally occurring in the subtropical zone although at times it ranges well down into the tropical zone or up to the lower temperate zone, but only where the vegetation is lush and dense, such as in cloud forest.



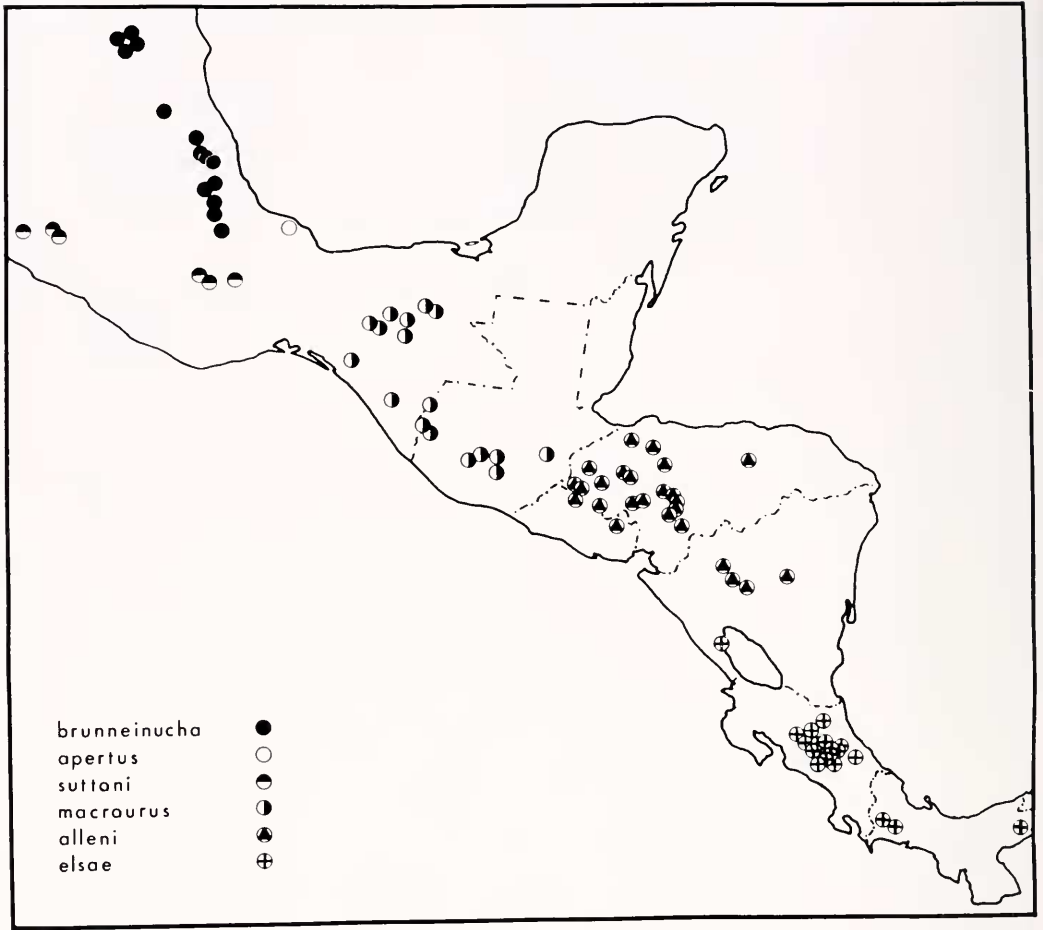


Figure 16. Northern races of *A. brunneinucha*.

At the northern end of its range, the species occurs as low as 200 m (nominate *brunneinucha* of eastern Mexico) and 350 m (*A. b. apertus* of the Sierra de Tuxtla, southern Veracruz) but on the other hand in the same area it also reaches an extreme altitude of 3,500 m (*A. b. suttoni* of Guerrero and Oaxaca).

This is doubtless the maximum altitudinal range for any species of atlatetes within a reasonably circumscribed area. In Central America, the species ranges from 550 to 3,400 m and in South America from 900 to 3,400 m. Throughout, however, it seems

most abundant between roughly 1,000 and 2,000 m.

Because of the abundance of moist subtropical forest, the species is widely distributed with few major discontinuities. As with birds of similar requirements, the species is absent in most of Panama, but it occurs throughout the Andes south to northern Peru where, owing to the absence of moist forests, it drops out on the western slope but continues southward on the eastern side.

In the coastal range of northern Venezuela there is an interesting transposition of

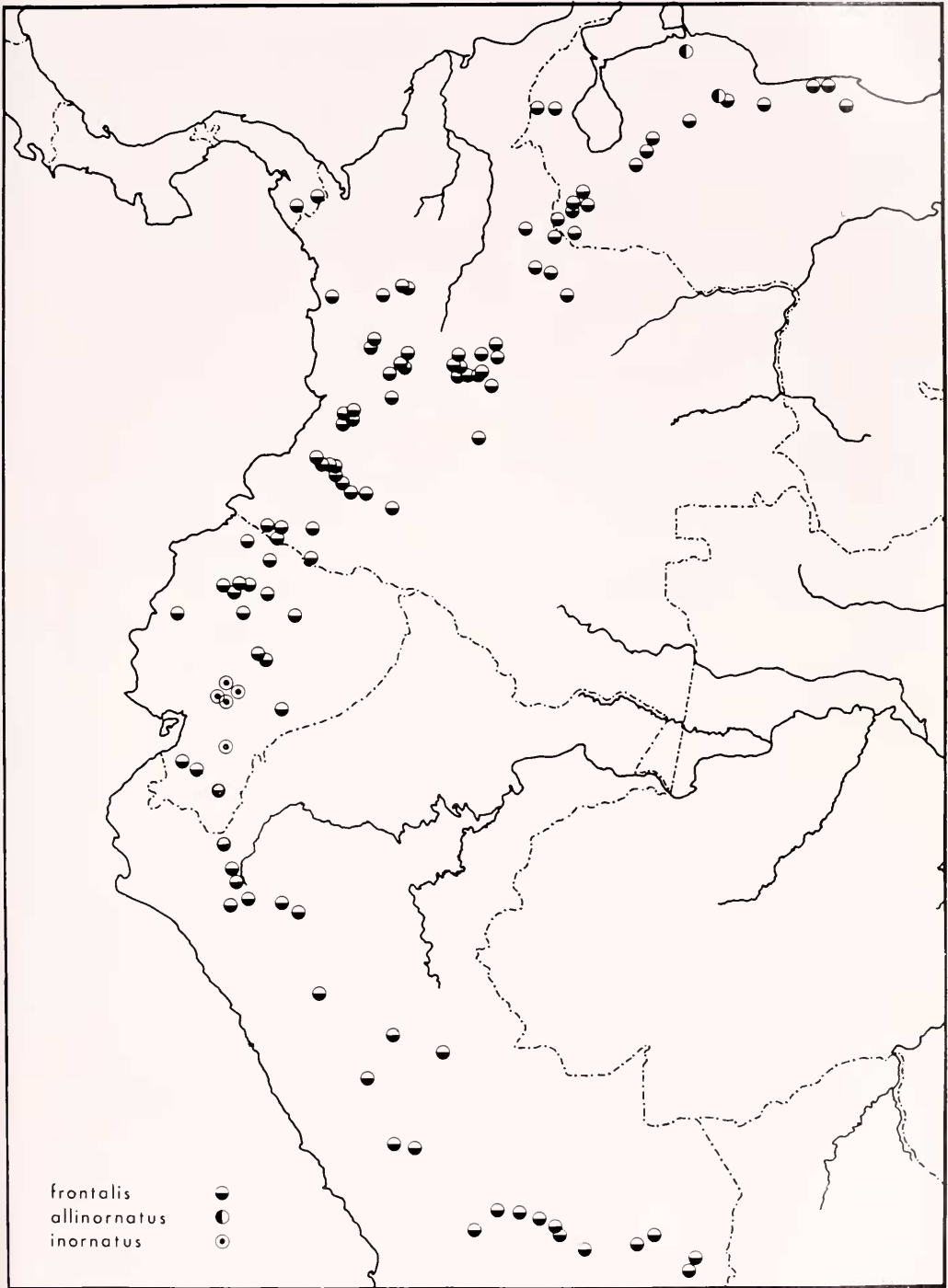


Figure 17. Southern races of *A. brunneinucha*.

relative altitudes between *A. b. frontalis* and *A. torquatus phaeopleurus*. Throughout their joint ranges, *A. torquatus* occupies the higher altitude and *A. brunneinucha* the lower, but at Rancho Grande, Aragua, *A. torquatus* ranges from 700 to 900 m while *A. brunneinucha* occurs from 900 to 2,400 m but its optimum range is between 1,600 and 2,000 m (Schäfer and Phelps, 1954).

*Habitat*.—The bird is an inhabitant of the interior of humid forest or of the thick undergrowth at the edges of the forest, but is still under taller trees. This propensity for the cover of forests has been remarked upon by Miller (1963) and Slud (1964). The latter also pointed out that in Costa Rica *A. gutturalis* [= *albinucha*] and *A. brunneinucha* have ranges in common but *A. albinucha* is a nonforest species. This dichotomy in habitats seems to hold throughout the ranges but no broadening of the habitat of *A. brunneinucha* seems to occur south of Colombia where *A. albinucha* is absent.

*Habits*.—The ecology of *A. brunneinucha* is fairly well known considering the difficulty in obtaining this information for other members of the genus. This is perhaps because, although a quiet species, it does not seem to be so shy as some other atlapetes.

As was noted long ago by Taczanowski (1884), and later by Carriker (1910), *A. brunneinucha* is usually found in pairs or in family groups. Schäfer and Phelps (1954) reported a maximum flock size of six.

*A. brunneinucha* is a bird of the dark forest floor, although Miller (1963) once found it 20 feet up in second-growth where it was feeding on seeds in company with tanagers. This, however, is probably an infrequent practice. Miller also comments on the bird's habit of kicking dry leaves in search of food, although Taczanowski (1884) reported that the species tossed the leaves with its beak. While in Venezuela and Peru, Fitzpatrick (in litt.) has seen the bird stir the litter with its feet but has never seen it use its bill for this purpose.

Miller (1963) believed that, in Colombia, breeding probably occurs throughout the year. Farther north, in Mexico and Central America, breeding seems to begin in March or as early as late February and extends to April or May or even June (Miller et al., 1957; Blake, 1958; Carriker, 1910). Breeding in Venezuela has been recorded from April to June (Schäfer and Phelps, 1954); in Peru the only breeding record known to me is that of a nest found in January (Taczanowski, 1884).

The nest, which is placed in shrubs or ferns close to the ground, is made of coarse leaves and lined with finer material (Taczanowski, 1884; Carriker, 1910). The clutch seems to consist of but one or two greenish or bluish white eggs (Sclater and Salvin, 1879; Carriker, 1910).

*A. brunneinucha* appears to be omnivorous (Olivares, 1969), although Taczanowski (1884) examined one specimen that had eaten only invertebrates.

As with all forms of *Atlapetes*, this species has an inconspicuous voice. Taczanowski (1884) described its call note as a series of rapid *tsit-tsit* notes and its song as reminiscent of the "voice" produced by a rubber doll; presumably this refers to "a series of high-pitched notes" (Peterson, 1973). Miller (1963), in spite of long-term observations in Colombia, never heard a song but described the infrequently produced alarm calls as chattering *tsip*'s and noted a mewling note suggesting that of *Pipilo chlorurus*.

*Morphological variation*.—Chapman (1923a) in his review of the genus *Buarremon* [= *Atlapetes*] pointed out that *A. brunneinucha* probably has a more extensive range than any other species of the subtropics and believed it exhibited no geographical morphological variation in spite of its wide distribution. Chapman did, however, recognize the taxon *inornatus* as being close to *brunneinucha* but, as was customary at that time, treated it as a full species rather than as a race of *A. brunneinucha*. Parkes (1954) in his review of the species detected more variation and rec-

ognized nine races, five of which he described. Subsequently two more races were named (Phillips, 1966; Rowley, 1968) bringing the total to 11 subspecies. There is no doubt that there is geographical variation within the species, but most of this variation is extremely subtle and probably not worth nomenclatural recognition.

There is some geographical variation in size (see Parkes, 1954, p. 134 for details). *A. b. frontalis*, the most widespread race of South America, has a slightly longer bill than all other populations, possibly excepting the races *inornatus* and *allinornatus* which are restricted to west-central Ecuador and central Venezuela, respectively. *A. b. suttoni* of Guerrero and Oaxaca and particularly *A. b. macrourus* of Chiapas and Guatemala have generally longer tails than the remaining populations. No geographical trend in these variations is evident.

Variations in color and patterns are also not pronounced. The extent of yellow bordering the chestnut crown varies somewhat, as does the amount of black on the forehead and what portion of the venter is occupied by either gray or white. Presumably these variations are of no biological significance. There is one characteristic, however, that does have a pattern, although its significance is also not apparent. This is the absence of a black breast band in three small, isolated or relatively isolated populations. One of the characteristic and striking markings of most taxa of *A. brunneinucha* is a black band that separates the white throat from the gray, or gray and white, chest and abdomen. In *A. b. apertus*, which is isolated in the Sierra de Tuxtla of Veracruz, Mexico, in *A. b. allinornatus* of the Sierra de San Luis and Sierra de Aroa in northwestern Venezuela, and in *A. b. inornatus* which occurs in a pocket on the western slopes of the Andes of central Ecuador, the black pectoral band is absent or rudimentary. The significance of this is unknown. The isolation of the three taxa leads one to suspect that the breast band is a species recognition character which might be unnecessary in

small or isolated populations. *A. b. apertus* lacks congeners nearby but both *A. b. allinornatus* and *A. b. inornatus* do have congeners in the vicinity. Some relationship between the lack of a breast band and the presence of closely allied *A. torquatus* also suggests itself, but *A. torquatus*, while near *A. b. inornatus*, is absent from the range of *A. b. apertus* and *A. b. allinornatus*. Furthermore, in Mexico and most of Central America, where *A. torquatus* is absent, *A. brunneinucha* has a breast band. Especially baffling is the fact that the width of the band does not vary appreciably between the populations that do possess it, which is contrary to what one might expect if this is especially important in inter- or intraspecific recognition in large populations. Parkes (1954) has pointed out that there is no way to resolve whether the banded or unbanded condition is ancestral to the other.

#### ***Atlapetes torquatus* superspecies**

There are 15 allopatric taxa that are very similar morphologically, that certainly are closely related, and that doubtless are best treated as members of a superspecies, viz., *A. torquatus*. The *torquatus* superspecies seems to be comprised of the allospecies *virenticeps*, *atricapillus*, and *torquatus*, but to which allospecies certain of the 15 taxa belong is a vexing problem, a circumstance not met with elsewhere in the genus. The root of the problem is the rather major morphological variation between a number of the 15 taxa, further complicated by the fact that variation occurs within several characters, and these variations are seldom concordant.

Except for the absence of a chestnut piteum, most forms of *A. torquatus* superspecies are notably similar to *A. brunneinucha*, a species which has about as extensive a range but which exhibits little geographic variation.

Within the *A. torquatus* superspecies there is some minor geographical variation in overall size and in the relative lengths of the wing and tail, and somewhat greater



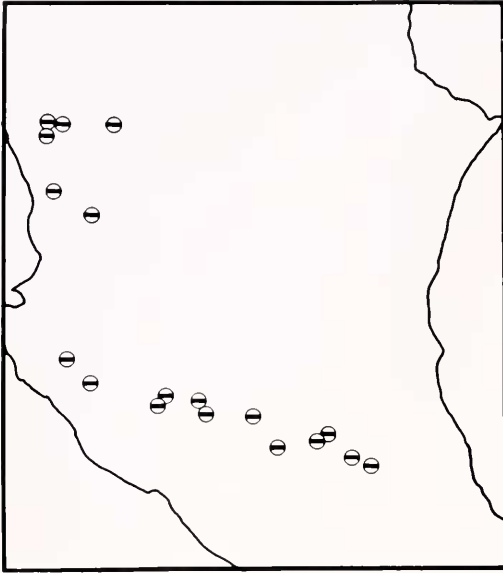


Figure 18. Distribution of *A. virenticeps*, of the Mexican plateau.

variation in the color of the venter, but larger differences occur in the pattern and color of the head, in the presence or absence of a pectoral band, and in the color and extent of the superciliary stripe. Two forms, *tacarcunae* and *atricapillus*, have markedly more robust bills.

There are three basic head types, viz. all black (*tacarcunae* and *atricapillus*), black with a medial stripe and superciliaries that are yellowish green (*virenticeps*), and black with a medial stripe and superciliaries that are either gray or white (the remaining 12 taxa). The geographical distribution of these three patterns is relatively simple (Fig. 20); *virenticeps* is in Mexico, *tacarcunae* and *atricapillus* are in eastern Panama and north-central Colombia, respectively, and the other forms occur, some in isolation and others contiguously, from Costa Rica to Argentina.

The distribution of taxa with or without breast bands is more complex (Fig. 20). The forms *virenticeps*, *costaricensis*, *tacarcunae*, *atricapillus*, *assimilis*, *nigrifrons*, and *borelli* lack the band; the remaining eight

taxa have it. In geographical terms this means that forms without breast bands occur in the northern part of the range, except for the Sierra Nevada de Santa Marta and the Venezuelan Andes, and in the extreme south, while forms with pectoral bands occur in the southern range, with the exception of southern Bolivia and northwestern Argentina which are occupied by *borelli*, a taxon without a band.

The color of the superciliaries (ignoring minor departures from these generalizations, such as white lores with gray stripes) is either (a) black (= absent), which is the case in black-headed *tacarcunae* and *atricapillus*, or (b) yellowish-green, as in *virenticeps*, or (c) gray, as in *costaricensis*, *basilicus*, *perijanus*, *larensis*, *assimilis*, *nigrifrons* and *poliophrys*, or (d) white, which is the condition in the five taxa remaining. The geographical pattern (Fig. 20) is even more complex than that which exists for pectoral bands. Agreeing with the pattern of distribution found for head color are *virenticeps* and also *tacarcunae* and *atricapillus*. White eye stripes occur in the outliers at both ends of the Andes, viz. *phaeopleurus* and *phygas* in north and northeastern Venezuela and *torquatus*, *fimbriatus*, and *borelli* in Bolivia and northwestern Argentina. The remaining taxa have gray stripes. From this distribution one might suspect the existence of some sort of relationship between outlying populations and white superciliaries, but this is dispelled upon recalling that *basilicus* of the Sierra Nevada de Santa Marta and *costaricensis* of Costa Rica and westernmost Panama are both completely isolated but have gray eye stripes. There exists no correlation between breast band and the color of the superciliaries; all five forms with white superciliaries have breast bands but of the seven with gray eye stripes, four have pectoral bands and three do not.

Chapman (1923b) was the first to attempt to determine the interrelationships of this perplexing complex of birds. However, this work was done when "mutations" had attracted the fancy of biologists and when



many phenomena were attributed to "mutations." We now know, however, that these phenomena have been brought about by a variety of less radical causes. Chapman, dealing with 13 taxa (*perijanus* and *larensis* had not been named at that time), treated the thick-billed, black-headed forms *atricapillus* and *tacarcunae* as conspecific, placed into one species the three taxa with no pectoral bands and gray superciliaries (*assimilis*, *nigrifrons*, and *costaricensis*), and treated each of the remaining forms as a full species. The later action was doubtless because of the prevailing belief that even obviously related taxa were to be considered distinct species unless morphological intergradation could be demonstrated.

Hellmayr (1938) maintained the two black-headed forms as one species (*A. atricapillus*) but lumped all other taxa into a single species, *A. torquatus*. He even included *virenticeps* of Mexico and pointed out that it was a distinctive form that closely resembled the immature of the more southern taxa.

The next to deal with the problem were de Schauensee and Eisenmann (de Schauensee, 1966) who proposed a quite different treatment. This made Mexican *virenticeps* a full species and *costaricensis* a race of *A. atricapillus* on the premise that *tacarcunae* of eastern Panama is morphologically intermediate between *costaricensis* and nominate *atricapillus*. All other forms were placed in *A. torquatus*. On geographical grounds this treatment is appealing, because it avoids the problem of explaining the distant isolation of *costaricensis* from other members of its species. Nevertheless, I cannot appreciate how *tacarcunae* can be considered to be morphologically intermediate between *costaricensis* and *atricapillus*. On the contrary, I find *tacarcunae* difficult to distinguish from *atricapillus* and to be well-differentiated from *costaricensis*.

The last attempt to resolve the problem (Paynter, 1970) resulted in the lumping of all taxa into a single species (*torquatus*). The reasoning behind this was based par-

tially on an uncritical acceptance of de Schauensee and Eisenmann's claim that *tacarcunae* was intermediate between *costaricensis* and *atricapillus* and partly on the belief that *atricapillus* and *assimilis* were geographically well separated. As explained above, *costaricensis* does not appear particularly close to *tacarcunae*. Also, since my earlier analysis, *atricapillus* and *assimilis* have been found (Olivares, 1969) within about 25 kilometers of one another, which is so close that it now seems a definite possibility that they may be parapatric.

I think that the best treatment is to recognize three allospecies within the superspecies *A. torquatus*. *A. virenticeps* is the first species. It appears to be a relict form which in its isolation has reverted to or (less likely) has retained some juvenile characteristics.

The second allospecies is *A. atricapillus*, with *tacarcunae* as a subspecies. Its completely dark head and thick bill, its relatively restricted range, its lower altitude (see below), and its apparent parapatry with *assimilis* suggest that this is an offshoot of the third allospecies, *A. torquatus*. *A. atricapillus* seems to have differentiated from its stem stock but has not progressed far enough to allow it to be ecologically compatible with *A. torquatus* or possibly to be reproductively isolated from it.

Into the third allospecies, *A. torquatus*, I place all the remaining taxa. The presence or absence of a breast band and the color of the superciliaries are probably characters that readily respond to isolation. They may have no adaptive significance, or they may be important in interspecific recognition. I am inclined to believe they are of little significance since, for example, one can see in the geographical continuum of *torquatus*, *fimbriatus*, and *borelli* successive stages in the loss of the pectoral band.

#### *Atlapetes virenticeps*

*Range*.—Occurs in the temperate zone of the southwestern portion of the Mexican Plateau and Pacific slope from Sinaloa south to Michoacán (Fig. 18). In the north

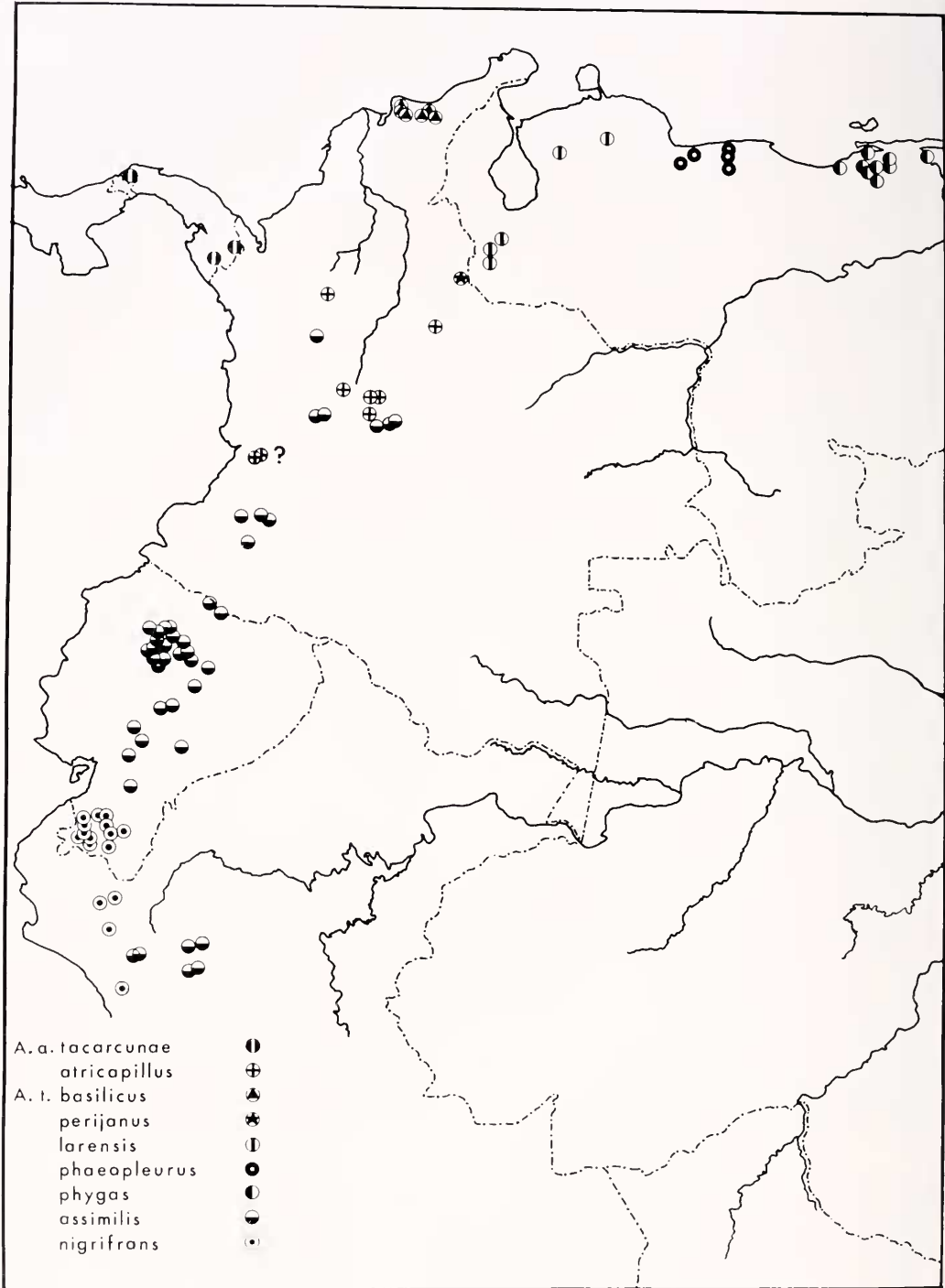


Figure 19. Distribution of *A. atricapillus* and the centrally located races of *A. torquatus*. Birds from the Western Andes have not been examined but are presumed to be referable to nominate *atricapillus*.

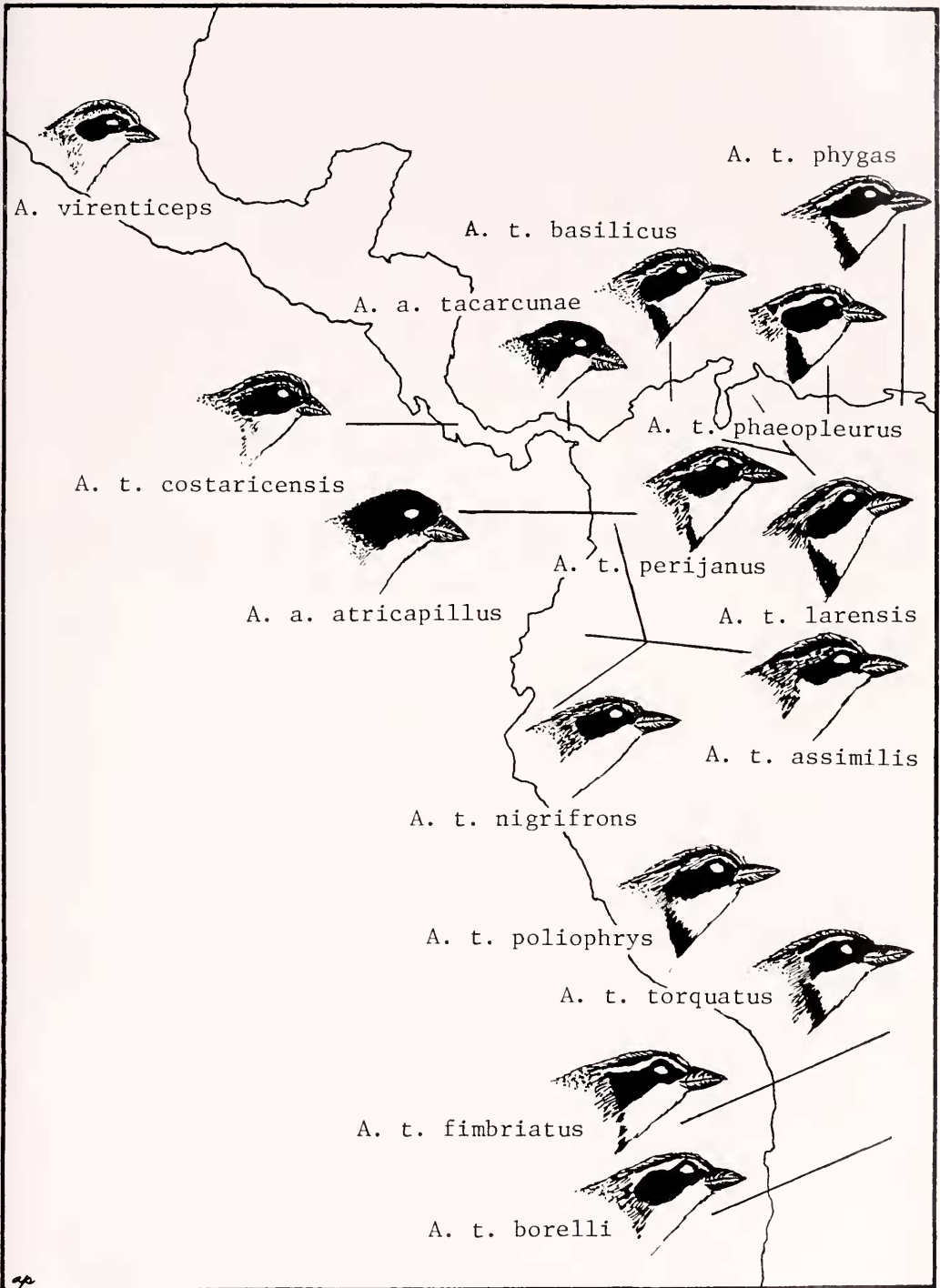


Figure 20. Color and pattern in the head and breast of the *A. torquatus* superspecies.

it ranges from about 1,100 to 1,900 m while farther south it occurs from about 2,000 to 3,600 m.

*Habitat*.—Thick undergrowth of oak or coniferous forests and at their edges (Edwards, 1972).

*Habits*.—Very little is known of the species. Schaldach (1963) reported behavior similar to that of towhees (*Pipilo*) in that the bird feeds in litter, turning over leaves in its search for food. Unfortunately, he was unable to determine whether the bill or feet were used for this activity.

Nesting and laying have been noticed in June and July (Miller et al., 1957; Schaldach, 1963). Schaldach (1963) believed the species to be doubled-brooded.

*Morphological variation*.—Some slight variation in color and size, perhaps not concordant with geography, seems to exist, but the pattern described by Moore (1938) and leading to his description of a northern race (*verecundus*) cannot be confirmed (Hardy and Webber, 1975).

### *Atlapetes atricapillus*

*Range*.—The species has been found on a few of the higher mountains of eastern Panama (east of the Canal Zone) and in Colombia in the middle Magdalena Valley on the eastern slope of the Central Andes and western slope of the Eastern Andes, once at the northern end of the Central Andes (above Puerto Valdivia, Antioquia) and, recently (Hilty, 1977) on the Pacific slope of the Western Andes between Cali and Buenaventura (Fig. 19). In all there are records from only about a dozen specific localities, all of which are at an altitude from about 700 to 1,500 m. Although various authors (e.g., Chapman, 1923b; Hellmayr, 1938) have said this is a species of the subtropical zone, its altitudinal range would seem to indicate it is a form of the upper tropical zone, to which the species was also ascribed by de Schauensee (1951).

*Habitat*.—Dense undergrowth in wet forest and edges (Ridgely, 1976).

*Habits*.—A breeding pair was collected at

La Vega, Cundinamarca (Olivares, 1969) but the date was not recorded. Nothing else has been published.

*Morphological variation*.—The birds of Panama were separated by Chapman (1923b) from the Colombian population on the basis of slight differences in color patterns and supposedly a longer, thicker bill. The only character I am able to recognize is a tendency for the western birds (*tacarcunae*) to have a barely distinguishable gray postocular line, in contrast to the solid black head of the nominate race.

The records of Hilty (1977) from the Western Andes have been tentatively assigned to the nominate form, although I have not examined the birds.

### *Atlapetes torquatus*

*Range*.—The range of allospecies *A. torquatus* is the most extensive of the three taxa within the superspecies. *A. t. costaricensis*, an isolate (Fig. 21), is found in southwestern Costa Rica and presumably in adjacent Chiriquí, Panama (Ridgely, 1976), but I can find no specific record for the latter. It ranges from about 1,100 m down to 300 m in the subtropical zone and upper reaches of the tropical zone. The species next appears in the Sierra Nevada de Santa Marta, Colombia, again as an isolate (*A. t. basilicus*), where it occurs from the upper tropical zone to the temperate zone (600 to 2,800 m) (Fig. 19).

*A. t. assimilis* has a wide but curiously disjoint range (Fig. 19). In Colombia it occurs on both slopes of the Eastern Andes, but only in the vicinity of Bogotá. (The species seems to be absent south of here, but this may be because of the lack of observations and north of Bogotá it is absent for about 300 km, until it recurs, as other races near the Venezuelan border.) *A. t. assimilis* is found on both slopes of the mid-portion of the Central Andes from near Medellín to about the Quindío Pass and then reappears on the west slopes in the vicinity of Popayán. The race also occurs near Popayán on the eastern slopes of the



Western Andes. From the Colombia-Ecuador border south to south-central Ecuador, *A. t. assimilis* is found on both sides of the Andes but in southwestern Ecuador and northwestern Peru the race is replaced by another (*nigrifrons*). In southeastern Ecuador the species seems to be totally absent, only to appear again (as *assimilis*) on the eastern slope of northern Peru. Some of the patchiness of the distribution is doubtless because of spotty collecting, but the broad pattern is probably as outlined. *A. t. assimilis* has an altitudinal range from about 1,500 to 3,600 m and is typically found in the temperate zone.

The outlying Andes of northeastern Colombia and of Venezuela are occupied, from south to north, by four races (*perijanus*, *larensis*, *phaeopleurus*, and *phygas*). They occur at altitudes from about 700 to 1,800 m in the subtropical zone and, apparently on occasion (at least in *phaeopleurus*), in the upper tropical zone (Schäfer and Phelps, 1954; also see discussion under *A. brunneinucha*, p. 344).

On the slopes of southwestern Ecuador and northwestern Peru there occurs *A. t. nigrifrons* with an altitudinal range from 600 to 2,700 m, which is considerably wider than that of *A. t. assimilis*. It is found from the upper tropical zone up to the beginning of the temperate zone.

The species seems to be absent from northern (except the extreme north) to central Peru. It reappears on the eastern slopes of central Peru and ranges from here through eastern Bolivia to northwestern Argentina in a series of four subspecies (*poliophrys*, *torquatus*, *fimbriatus*, and *borelli*). These generally occur in the temperate and subtropical zones in the north but are restricted to the subtropical zone in the south (Fig. 22). There is, of course, a corresponding drop in altitudinal ranges from north to south (*poliophrys*, ca. 1,800–3,650 m; *torquatus*, ca. 2,000–3,100 m; *fimbriatus*, ca. 700–3,050 m; *borelli*, ca. 400–1,200 m).

From this survey, it is evident that the

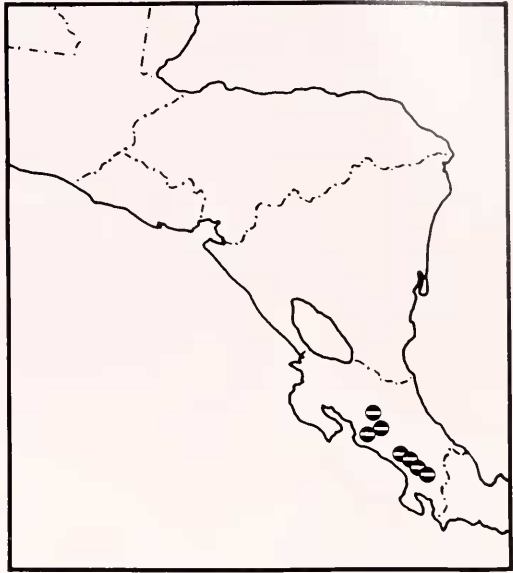


Figure 21. Distribution of *A. torquatus costaricensis*.

subspecies of *A. torquatus* generally frequent the subtropical zone and quite regularly reach the tropical zone. The one exception to this is *A. t. assimilis* which is strictly a temperate zone form.

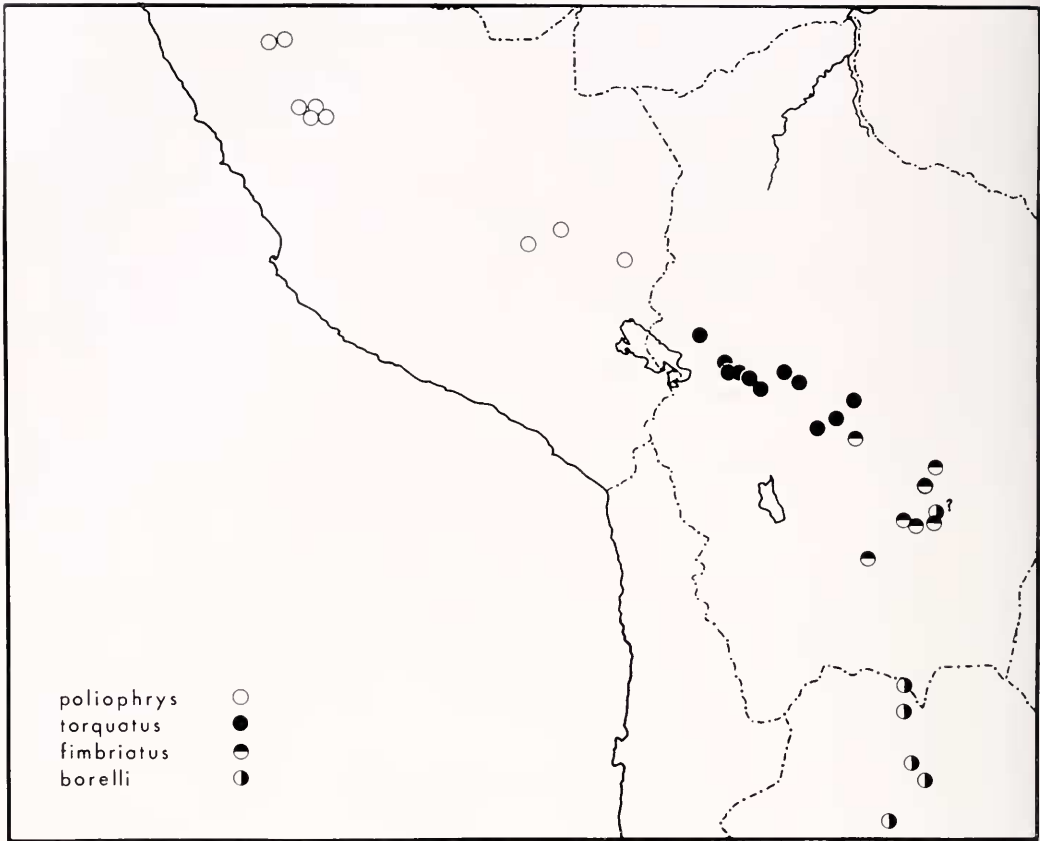
*Habitat*.—*A. torquatus* is a species of thick second-growth and other dense vegetation in fairly humid areas. Slud (1964) pointed out that in Costa Rica *A. brunneinucha* prefers heavy growth within tall forest, and *A. gutturalis* [= *albinucha*] selects brush in the open, while *A. torquatus* occupies the bushy borders of forests, an intermediate habitat. My observations of these species in Mexico and Ecuador confirm this.

*Habits*.—Skutch (1954) has written a brief life history account of this species in Costa Rica.

*A. torquatus* frequently occurs alone or in pairs, in contrast to the somewhat more gregarious species such as *A. rufinucha*, *brunneinucha*, or *schistaceus*, although at times it does occur in moderate-size groups.

In Ecuador on several occasions, I have observed the species foraging on the ground and turning leaves with its bill. I have never



Figure 22. Southern races of *A. torquatus*.

seen it use its feet for this purpose. Skutch (1954) also commented on this use of the bill and noted that the bird feeds on small invertebrates and at times eats decaying leaves.

Its voice is thin and weak. In Ecuador, I noted a song as *zeep, which-a-weet*, with the tone dropping on the *a* and rising on the *weet*. Skutch (1954) notes that the song is given from, or close to, the ground and describes the male's song as being squeaky, high-pitched, tuneless, and rapid; the female's song is similar but even weaker. I noted two calls in Ecuador, a high, metallic, *zeep* and a soft throaty *chuck*. Skutch (1954) described the call as similar to that given by a Cardinal (*Cardinalis cardinalis*). Slud (1964:383) described the voice as an

insect-like trill or as the "tinkling of a fine silver chain"; he also noted a *cherr* which must be what I described as *chuck*.

Breeding in Costa Rica is from February to September (Skutch, 1954), in northern Venezuela it is from May to July (Schäfer and Phelps, 1954). There is no information from farther south. Skutch (1954) noted that the species builds a bulky nest in dense tangles from one to six meters above the ground; two white or very pale blue eggs are laid and incubated only by the female.

*Morphological variation.*—As has been discussed above, morphological variation is extensive within *A. torquatus*. The pectoral band appears in *basilicus*, *perijanus*, *phaeopleurus*, *phygas*, *larensis*, *poliophrys*, *torquatus*, and *fimbriatus* (faint) and is absent

in *costaricensis*, *assimilis*, *nigrifrons*, and *borelli* (Fig. 20). Because of the irregular distribution of this character, one is led to suspect that the absence of the pectoral band might be related to sympatry or parapatry with *A. brunneinucha*, the species that *A. torquatus* so closely resembles morphologically, as well as in behavior and altitudinal distribution. However, no correlation can be found.

The color of the superciliary is about equally divided between races with gray stripes and races with white stripes (Fig. 20). The northeastern and southern Andean forms have white superciliaries; *nigrifrons* of southwestern Ecuador and northwestern Peru has a gray superciliary with white lores; the remaining taxa have gray superciliaries. This pattern does not seem to be related to the presence or absence of a pectoral band, or to be correlated with contact with other species of *Atlapetes*.

There is considerable, but not extreme, variation in the color of the flanks and undertail coverts (gray-green, brownish, etc.) and the extent to which this color suffuses the white belly. There are also minor variations in the width and length of the medial head stripe and in the color of the back and tail. No patterns in these variations are recognizable.

Males are slightly larger than females, but I am unable to detect any significant difference in size (wing, tail, culmen) between like sexes of the various races for which I have adequate series of specimens (*costaricensis*, *basilicus*, *assimilis*, and *nigrifrons*); measurements of specimens in the remaining races all fall within the ranges noted in the four large series. I conclude that if there are racial differences in size they are doubtless very small and certainly of no biological significance.

## ORIGIN AND INTERRELATIONSHIPS OF THE TAXA

### Introduction

It is now generally believed that the exceptional abundance of Neotropical avian

species, as well as that of other animals and plants, is mainly the result of Pleistocene fluctuations in both temperature and precipitation. These climatic changes resulted in the expansion and contraction of forests and grasslands in the lowlands, as well as in vertical shifts in biomes in the mountains. These changes, in turn, led to the shrinkage and even disappearance of some populations during one phase of the cycle while during the alternate phase the populations expanded their ranges. Species differentiated to various degrees, disappeared, or remained unaltered during the restrictive phases while in the expansive stages they kept their identity, were absorbed by other populations, disappeared altogether, or even further differentiated. Over the course of several cycles of varying duration and intensity, the opportunities for permutations were enormous so that now, at best, only broad patterns of speciation or those of recent occurrence can be discerned.

This theory has been developed principally by Haffer (for a summary see Haffer, 1974), who has applied it mainly to the tropical lowland forest avifauna. He has postulated 16 major areas in Central and South America that served as forested refugia for birds during the most arid periods of the Pleistocene. Because climatic fluctuations affected the mountains as well as the lowlands, it was not surprising when in a study of the *Atlapetes schistaceus* species-group (Paynter, 1972) it became evident that some subtropical/temperate zone taxa seemed to have had their origin in close proximity to the lowland refugia postulated by Haffer. Furthermore, it was also apparent that the origin of certain other taxa could be explained only if there had existed additional refugia in pockets on the slopes of the mountains.

The present study completes the review of the genus *Atlapetes* and refines and expands some of the zoogeographic concepts developed earlier.

The 24 species that constitute *Atlapetes* fall into four natural subunits that reflect

the evolutionary history of the genus. The order in which these four subunits are treated below is intended to show a general trend from the most "typical" atlapetes to those that approach other emberizine genera. However, because a linear arrangement sometimes does not permit all related taxa to be near one another, and because even the limits of emberizine genera are fuzzy, only the grouping of the species within the units should be considered as significant.

### ***Atlapetes albinucha* superspecies**

Two allospecies comprise this superspecies, *A. albinucha* of Mexico, Central America, and Colombia and *A. pallidinucha* of Colombia and Ecuador.

#### *ATLAPETES ALBINUCHA*

*A. albinucha* has eight races (Figs. 3, 4). Two (*coloratus* and *azuereensis*) have been described from Chiriquí and Veraguas, western Panama, and are almost certainly inseparable from *brunnescens*, also from western Panama. Five of the remaining races (*griseipectus*, *fuscipygius*, *parvirostris*, *brunnescens*, and *gutturalis*), ranging from southwestern Mexico to Colombia, differ only slightly from one another, while nominate *albinucha* of eastern Mexico is distinctly different, having a completely yellow venter rather than only a yellow throat. Although distinctive, this is believed to represent a small genetic difference (see p. 330).

The sharp, albeit relatively minor, discontinuity in phenotype displayed by *A. a. albinucha*, in contrast to the very minor and intergrading morphological variation in the remaining races, even including *A. a. gutturalis* of Colombia which is isolated from the Middle American populations by a sizable gap in eastern Panama, is provocative. This suggests that *A. a. albinucha* may have been isolated from the southwestern Mexico

and Central American populations for considerable time, or at least more completely. And, conversely, it could indicate that the isolation of *A. a. gutturalis* may have been more recent, or less complete.

Climatic changes in the Pleistocene might account for this pattern. During the height of a glacial period, when the vegetation zones were lower, a population may have been isolated in the lowlands of eastern Mexico, possibly only north of the Isthmus of Tehuantepec but more probably spanning the Isthmus of Tehuantepec to northeastern Chiapas as well; the latter distribution would explain the present occurrence of morphologically similar populations on either side of the Tehuantepec lowlands (see Fig. 3). In isolation the northern population either differentiated into distinctive nominate *A. albinucha* or, more probably, simply did not change appreciably, thereby retaining its similarity to *A. pallidinucha*, its South American allospecies (see p. 335).

On the other hand, during the Pleistocene glaciations the low mountains of eastern Panama, which now lack subtropical vegetation, except for a limited area on Cerro Tacarcuna, and which are not now occupied by this species, probably had a suitable habitat. The presence of subtropical vegetation provide a series of stepping stones facilitating exchange between the Central America and Colombian populations. The populations of Central America proper were at lower elevations than today and probably were more nearly contiguous with one another than they are now. This would account for their morphological similarity which also suggests that their present isolation is fairly recent. In addition, the Colombian population doubtless was farther west than now, owing to its presence on the "discontinuous mountain bridge" (Haffer, 1974:15) which connected the Western Andes and the mountains of Darién, across what is now the lower Río Atrato valley.

With the amelioration of the climate, the low mountains of eastern Panama lost their

subtropical vegetation and became unsuitable for the species. The Atrato "mountain bridge" also disappeared and the species retreated to the Andes. These events resulted in a wide distributional breach. Meanwhile, the subtropical zone moved higher in the mountains of Chiapas. This shift allowed the eastern and western populations to move closer together. This teeter-totter effect would, therefore, bring the northern isolate closer to the main body of the species while at the same time it would progressively increase the isolation of the southernmost population. This seems to be a reasonable explanation for the unusual pattern of morphological variation now seen.

#### *ATLAPETES PALLIDINUCHA*

*A. pallidinucha* generally resembles *A. a. albinucha*. The principal difference is the presence in *A. pallidinucha* of yellow lores, an orange wash on the anterior part of the central crown stripe, and, ventrally, faint green striations, suggesting the plumage of immature birds. The more southern forms of *A. albinucha* differ more markedly in that the yellow of the venter is confined to the throat.

*A. pallidinucha* occurs in the Eastern and Central Andes of Colombia and south to central Ecuador, and just reaches Venezuela (Fig. 5). In South America *A. albinucha* is found on all three ranges of the Colombian Andes, but in the Eastern Andes it is not north of Cundinamarca (Fig. 4). (Neither species has been recorded in the Eastern Andes south of the vicinity of Bogotá, but this seems merely to be because of the absence of collectors; the southern portion of the Eastern Andes are very poorly known; see Fig. 1.) The two species have, therefore, overlapping ranges in the Central Andes and in the midportion of the Eastern Andes. They are, however, altitudinally segregated with *A. pallidinucha* in the temperate zone, or higher, and *A. albinucha* in the subtropics.

There are approximately 50 sites within the zone of overlap where either one or the other of the species has been recorded. At only one site have both been reported. This is at La Aguadita, Cundinamarca, at an altitude of about 2,000 m (Olivares, 1969). This location is on the steep western slope of the Eastern Andes. Altitudes exceeding 3,400 m are only a short distance from La Aguadita. Presumably the two species are segregated altitudinally within the region but were imprecisely cited as having come from the same place.

#### INTERRELATIONSHIPS

The morphological similarity and altitudinal segregation of these two species suggests that they are related but ecologically incompatible. I consider them, therefore, to be members of a superspecies. The resemblance of the Mexican race of *A. albinucha* to *A. pallidinucha* of South America, or conversely the greater dissimilarity between the two species where they are altitudinally parapatric is suggestive. It may indicate that nominate *A. albinucha*, the Mexican race, is a little-changed offshoot from the same stem giving rise to *A. pallidinucha*. The other races of *A. albinucha*, or at least the stock for these, may have arisen while in proximity to *A. pallidinucha* and, therefore, diverged more than did nominate *A. albinucha* which was far to the north.

I have postulated above (p. 354) that the race of *A. albinucha* in Colombia (*A. a. gutturalis*), although well-isolated from the Central American populations of the species, is morphologically similar to these populations because this isolation is relatively recent. On the other hand, the Mexican race, *A. a. albinucha*, which is narrowly isolated from another population, is morphologically distinct because it is an older isolate that only recently has come in near contact with another population.

The postulated origin of the races of *A.*



*albinucha* and the origin of the allospecies *A. albinucha* and *A. pallidinucha* can be reconciled as follows. Presumably the species had their origin during a dry period in the Quaternary when an ancestral population became divided between two (or more) forest refugia. Probably *A. pallidinucha* formed in a refuge at the head of the Central and Western Andes (the Caribbean Colombian or Nechí Refuge of Haffer, 1974). The other allospecies, *A. albinucha*, may have been formed in isolation in a refuge on the Pacific side of the Western Andes (Pacific Colombian, or Chocó, Refuge) or, even more probable, in Central America in the Caribbean Central American or in the Caribbean Costa Rican Refuge (all refuge names from Haffer, 1974), or possibly in a refuge in Mexico north of the Isthmus of Tehuantepec. Later with the amelioration of the climate the two forms moved out from their centers of origin and came into contact. They had not diverged much from one another, either morphologically or ecologically, but they were sufficiently differentiated so that they were reproductively isolated and retained their identity. There may have been parapatry, or partial sympatry, or, more likely, some altitudinal overlap with *A. pallidinucha* the higher taxon. In any case this may have resulted in further divergence between the two similar species. *A. pallidinucha* may have been prevented from ranging into Central America because of the lack of temperate forest on the low mountains. During the next phase of the climate cycle *A. pallidinucha* may have withdrawn to the Nechí Refuge, or even to the Napo Refuge of eastern Ecuador, and another population was isolated in the Eastern Cordillera of Colombia; here the two existing races differentiated. Meanwhile, *A. albinucha* pulled back to two or more refugia, the northern one (probably in Mexico) holding the population which had been farthest from the zone of contact with *A. pallidinucha* and a southern refuge in Central America or northwestern Colombia, with a

population which had been in contact with *A. pallidinucha*. This isolation allowed *A. albinucha* in its southern refuge to consolidate morphological and ecological divergencies brought about because of competition with *A. pallidinucha*, while the population in the northern refuge remained relatively stable in appearance, having been far away from the zone of contact with *A. pallidinucha*. During the next warm-moist period (the current one?) the population in the northern refuge (*A. a. albinucha*) moved higher in the mountains of southeastern Mexico, but was unable to cross the low Río Grijalva valley in Chiapas. The population in the Central American refuge spread throughout much of Central America and across into Colombia, later abandoning eastern Panama as the climate warmed and subtropical vegetation disappeared. Because of its attenuated range, clinal morphological changes have developed, resulting in the weakly differentiated races now recognized.

Although *A. pallidinucha papallacta* is remarkably similar to *A. rufinucha baroni* (see p. 334), I do not believe they are particularly closely related.

#### ***Atlapetes rufinucha* species-group**

The 11 species within this group are presumed to have had a common origin, although all do not seem to have split off at the same time. With only one or two exceptions, and these are based on doubtful records, none of the species is sympatric with any other member of the species-group, which, of course, lends credence to the belief that this is a natural assemblage of closely related taxa.

#### ***Atlapetes rufinucha* superspecies**

This superspecies is composed of *A. rufinucha*, a widespread polytypic species, and *A. melanocephalus*, a monotypic endemic of the Sierra Nevada de Santa Marta, the isolated massif in northern Colombia.



*ATLAPETES RUFINUCHA*

*A. rufinucha* is the most widespread of the 11 species within the species-group, occurring from westernmost Venezuela to Bolivia. There are a number of gaps in its range (Figs. 6, 7). While it is present in the Sierra de Perijá, a northward extension of the Eastern Andes on the Venezuela-Colombia border, it has not been found in the Eastern Andes except for a few dubious records from "Bogotá" (*A. r. simplex*, known only from native "Bogotá" specimens). It does not occur on the eastern slope of the Central Andes, but is found at the northern tip of this range, as well as on its western slope at the head of the Cauca valley. In the Western Andes, it is found only on the eastern slope, also far up the Cauca valley.

In Ecuador it is distributed on both slopes, but is absent for about 250 km in the central portion of the eastern slope. The species ranges a short distance down the western slope of northern Peru and in the east reaches central Peru. There is then a gap before the species recurs in southern Peru and eastern Bolivia.

Its ecological requirements are broad. It occurs in the subtropics, sometimes in the temperate zone, and in dry to moderately moist vegetation. Its altitudinal range is also notably extensive, covering about 3,000 m. In general this is a common and abundant bird, as one would expect from its tolerance of a wide range of ecological conditions. Unfortunately, the versatility of the species makes it impossible to speculate on its place of origin. The gaps in its distribution, however, are valuable clues in reconstructing the history of other species in this species-group (see *A. tricolor* superspecies, *A. albofrenatus*, and *A. leucopis*).

*ATLAPETES MELANOCEPHALUS*

*A. melanocephalus* is the second allospecies of the *rufinucha* superspecies. It is one of the two atlapetes in the isolated Sierra Nevada de Santa Marta (Fig. 8) and is closely allied to *A. rufinucha* and might

even be considered a particularly well-marked race of that species. It differs from *A. rufinucha* in having a fully black head (not chestnut), a black chin and upper throat, and silvery ear coverts. These characters are found in varying degrees in some races of *A. rufinucha* (see Table 1). For example, the black of the chin and throat occurs in *A. r. melanolæmus*. Also, in *A. r. phelpsi*, the race nearest to Santa Marta, there is a broad black band on the forehead and along the sides of the head which seems to be a step toward a fully black head; its ear coverts are nearly as silvery as in *A. melanocephalus*.

## INTERRELATIONSHIPS

There seems little doubt that *A. melanocephalus* had its origin in *A. rufinucha*, and probably from stock from which arose *A. r. phelpsi*. It is probably the youngest species within the *A. rufinucha* species-group.

*A. melanocephalus* occurs from the upper tropical zone (600 m) through the subtropical zone (2,400 m). It is the only member of the species-group to occur so low. Although this altitudinal range coincides with that of *A. torquatus* on Santa Marta, *A. melanocephalus*, if it is like *A. rufinucha*, is probably more arboreal and, therefore, is not ecologically competitive with it. There are no additional atlapetes on Santa Marta and presumably this allows *A. melanocephalus* a wider range in altitude than is usual in the genus.

*Atlapetes tricolor* superspecies

The three allospecies of this superspecies are morphologically very similar, the principal difference being in the color of the crown, which in *A. tricolor* is gold, in *A. flaviceps* is yellow, and in *A. fuscolivaceus* is blackish. Immature *A. tricolor* has a dull crown, resembling that of adult *A. fuscolivaceus*; no immature examples of *A. flaviceps* are known. Interestingly, immature *A. rufinucha* bears a strong resemblance to *A.*

*tricolor*, suggesting a relationship between the two taxa. The distribution of the two species (see below) further strengthens this belief.

#### ATLAPETES TRICOLOR

*A. tricolor* has an extended range (Fig. 9), beginning on the western slope (and one doubtful record for the eastern slope) of the Western Andes of Colombia and extending down the western slope of Ecuador, but becoming very sparse in the south, presumably because of increasing aridity. It reappears on the eastern slope in central Peru, after a gap of about 1,000 km. It occurs from the humid upper tropical zone to the upper subtropical zone in the north and in the subtropical and temperate zone in Peru.

#### ATLAPETES FUSCOOLIVACEUS AND *A. FLAVICEPS*

Both *A. fuscoolivaceus* and *A. flaviceps* have very restricted ranges on the eastern slope of the Central Andes (Fig. 9). *A. flaviceps* occurs in a deep valley on the south slope of Nevada de Tolima and *A. fuscoolivaceus* at the headwaters of the Río Magdalena in a cul de sac where the Eastern Andes swing abruptly west to join the Central Andes. Both species are known only from the subtropical zone. There has been little ornithological work on the east side of the Central Andes; it is possible that the ranges of these two species may be more extensive than now known.

#### INTERRELATIONSHIPS

*A. flaviceps* and *A. fuscoolivaceus* appear to be remnant offshoots of the stock that produced *A. tricolor*. Presumably ancestral *A. tricolor* was once confined to the Pacific Colombian (or Chocó) Refuge, as defined by Haffer (1974), and later expanded its range down the western slope of Ecuador, crossing over to the east at the low passes in southern Ecuador and northern Peru. A

subunit of the same ancestral stock seems also to have been restricted to the eastern side of the Central Andes, perhaps in the Caribbean Colombian (Nechí) Refuge. During a warm-moist period, it may have spread up the Magdalena valley along the eastern slopes of the Central Andes, only to retreat later to one area at the head of the valley, where *A. fuscoolivaceus* is now found, and to another restricted region 300 kilometers to the north, where *A. flaviceps* occurs.

The reason why *A. fuscoolivaceus* and *A. flaviceps* are restricted to two small areas doubtless is related to the wetness of the subtropical habitat at these points. Both places are at the head of valleys which are cut deep into the Andes. Presumably these regions receive much more precipitation than points that are farther east, away from the mountains, and nearer the arid upper Magdalena valley. Thus both species are probably unable to move down the valleys or up over their sides because of unsuitable habitats. These two places are certainly not the only sites with moist subtropical vegetation along the entire eastern slope of the range. Future work may reveal additional populations in pockets at the heads of other deep valleys.

#### GEOGRAPHICAL DISPLACEMENT

The wide geographical breach between the subspecies of *A. tricolor* is puzzling, as is the absence of the species on the eastern slope of Ecuador. Displacement by another species would seem an explanation. *A. rufinucha*, which in immature plumage is similar to *A. tricolor*, appears a likely species. The races *A. r. baroni* and *latinuchus* more or less fill the breach on the eastern slope from southeastern Ecuador to central western Peru (Fig. 6). *A. t. tricolor* then occurs from central to southern Peru, and this is followed by two races of *A. rufinucha* ranging from southern Peru to southeastern Bolivia (Figs. 7, 23). Although this would appear to be a classical example of a geographical replacement, there are some

flaws, the most important being that in general the species are found at different altitudes. In western Colombia and Ecuador, the two species have generally overlapping ranges, but *A. tricolor* is invariably at lower elevations. If the two species are competitors, one would expect that in the absence of one, the other might expand its altitudinal range. However, *A. rufinucha* in eastern Ecuador, where *A. tricolor* is absent, has the same vertical range as it does in western Ecuador, where *A. tricolor* is found. In Peru *A. t. tricolor* is at moderately higher elevations than is *A. t. crassus* in Colombia and Ecuador and, therefore, it occupies the lower part of the altitudinal range of *A. rufinucha*. In other words, *A. tricolor* seems to have expanded slightly upward in the absence of *A. rufinucha*. I can find no evidence that *A. rufinucha* drops to lower altitudes in Peru where *A. tricolor* is lacking; it does, however, occur as low as 600 m in Bolivia. Unfortunately, there are available only about 100 records for both species in a range covering over half the length of the Andes. While broad outlines of altitudinal preferences are obtained, it is hardly likely that more subtle differences in altitude between species and races will be revealed by these few data.

The manner in which *A. tricolor* replaces *A. rufinucha* and the resemblance of immature *A. rufinucha* to *A. tricolor* lead to the conclusion that the two are members of the same species-group. It follows that if *A. tricolor* is a member of the species-group then its allospecies, *A. flaviceps* and *A. fuscolivaceus*, must also be in the group. The presence of these two species on the eastern slope of the Central Andes, occupying a gap in the range of *A. rufinucha*, further reinforces the belief that these are indeed members of a closely related assemblage.

#### *Atlapetes albofrenatus*

*A. a. albofrenatus* is one of the most distinctive taxa of the *A. rufinucha* species-group by virtue of its white throat, heavy

malar streaks, and green back; however, in the race *A. a. meridiae*, the white throat and heavy streaks are reduced, and the bird is much less distinctly different from *A. rufinucha*. In any case, these characters are minor. The placement of *A. albofrenatus* in association with *A. rufinucha* is reinforced by two points. First, this is an active bird whose behavior is similar to that of *A. rufinucha* in contrast to the slower, more secretive movements of most atlapetes. Second, and more important, the species occurs within a breach in the range of *A. rufinucha* in the Eastern Andes from Bogotá north to southwestern Venezuela (Fig. 23). Of particular note is the fact that it does not occur in the Sierra de Perijá, the northward projecting spur of the Andes which is occupied by isolated *A. r. phelpsi*, but it does cross the barrier created by the depression formed by the Río Torbes, which separates the Eastern Andes from the Andes of Mérida. The only possible instance of sympatry is in the vicinity of Bogotá where *A. r. simplex* is said to occur, but this race is known only from several native "Bogotá" specimens and certainly comes from elsewhere, probably in the little-known Eastern Andes south of Bogotá. The altitudinal range of *A. albofrenatus* is somewhat more restricted than that of *A. rufinucha*, but the species displays the same versatility in habitat preference.

Thus there is no doubt that *A. albofrenatus* is related to the *A. rufinucha* species-group. Its relative distinctiveness indicates it is not part of the *A. rufinucha* species branch, but was derived from the same stock that produced *A. rufinucha*. It would seem to have originated in the Eastern Andes, simply because that is where it is now found. No Pleistocene refuge for subtropical forest forms has been proposed in the area now occupied by *A. albofrenatus*, although Haffer (1974) believes one existed farther north (the "Catatumbo Refuge"). The western slopes of the Sierra Nevada del Cocuy, the highest peak in the Eastern Andes, may have served as refugium. The

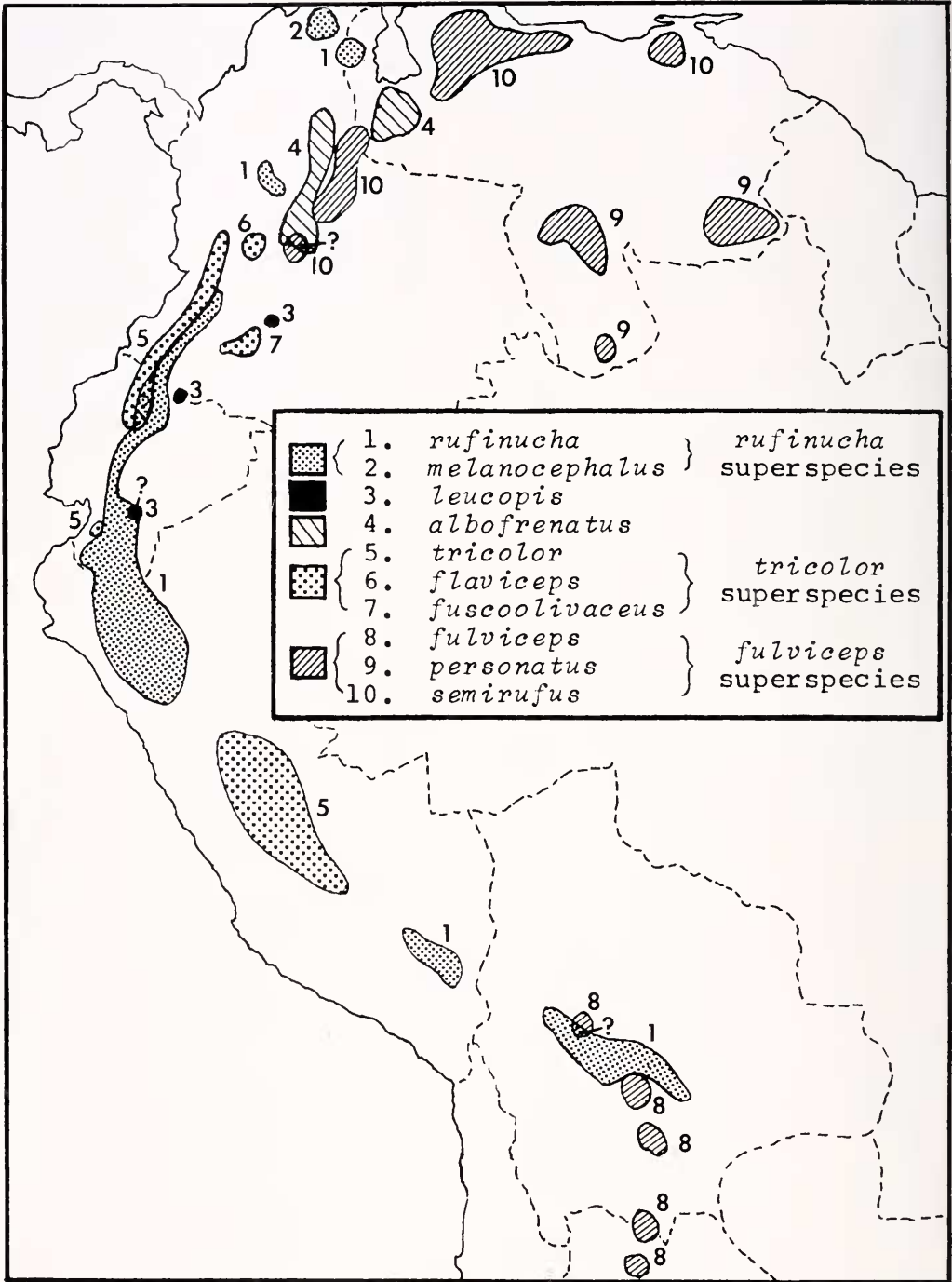


Figure 23. Geographic replacement within the *A. rufinucha* species-group in South America. Areas of doubtful sympatry are marked "?".



mountain is at the head of the long and arid Chicamocha valley running west to the Magdalena and may have caught moisture during dry periods and served as a refuge for forest inhabitants, even if the valley itself was arid. This is the region occupied by nominate *A. albofrenatus*. On the other hand, the fact that *A. albofrenatus meridae*, the race of the Mérida Andes, is less distinct from *A. rufinucha* than is *A. a. albofrenatus*, suggests that the Mérida Andes may have served as the initial isolation area and that the species later crossed the Río Torbes barrier where it further differentiated. Both hypotheses could be embellished, but there seems no way to establish which area could have served as a speciation center. Indeed, *A. albofrenatus* may be a relict and not autochthonous to either place.

#### *Atlapetes leucopis*

As I have observed before (Paynter, 1970), *A. leucopis* resembles *A. rufinucha melanolaemus* of Peru, the most distinctive race of *A. rufinucha*, except for its much larger size, white eye ring and eye stripe, and green underparts.

It seems to be sympatric with *A. rufinucha* at Palmas, Azuay, on the eastern slope of Ecuador, but does not coexist at the other two localities from which it is known, viz. La Plata, Colombia, which is on the east side of the Central Andes and Cerro Pax, on the east slope in southern Colombia (Fig. 23). The Palmas locality is suspect, however. The single bird from there was obtained by M. Olalla (Berlioz, 1932), a member of the family of professional collectors that is noted for inaccurately labeled specimens. From a few hours spent at Palmas, I know, that *A. rufinucha*, which Olalla also records from here, does indeed occur at this locality; I believe that *A. leucopis* may be somewhere in the general region but not sympatric with *A. rufinucha*.

The two Colombian sites for *A. leucopis* are to the east of the range of *A. rufinucha*

and the Ecuadorian locality is at the northern edge of the range of *A. rufinucha*, which reappears again about 250 kilometers farther north in Ecuador. Thus it seems that *A. leucopis* is a geographical replacement for *A. rufinucha*, although it is possible that allopatry may break down in Azuay at the southern end of the range of *A. leucopis* and the northern end of the range of *A. rufinucha*.

*A. leucopis* is not known to be sympatric with any other member of *A. rufinucha* species-group, but it should be noted that *A. fuscolivaceus* occurs in Colombia at Moscopán (alt. 2,400 m), Huila, which is only 32 km west of La Plata (alt. 2,350 m), and in the same valley.

It would seem that *A. leucopis* bears a relationship to *A. rufinucha* similar to that existing between *A. rufinucha* and *A. albofrenatus*, i.e., *A. leucopis* appears to have arisen from the same ancestral stock as *A. rufinucha*, but it is not a derivative of *A. rufinucha*. It is not possible to speculate on its place of origin.

#### *Atlapetes pileatus*

*A. pileatus*, the Mexican endemic (Fig. 12) is a small pallid version of *A. rufinucha*. It is isolated from the remainder of the species-group by all of Central America. It appears to be a relict that originated in Mexico or Central America, but it is not possible to speculate further.

#### *Atlapetes fulviceps* superspecies

There are three allospecies within the *A. fulviceps* superspecies, viz. *A. fulviceps*, *A. personatus*, and *A. semirufus*. All are morphologically very similar inhabitants of the subtropical zone, and all have a marked resemblance to *A. rufinucha*, but differ from *A. rufinucha* in that the black of the sides of the head is replaced by chestnut and, in some taxa, the chestnut extends to the throat and breast. *A. fulviceps*, which is monotypic, is found in Bolivia and northwestern Argentina (Fig. 14). *A. personatus*, with six well-



marked races, occurs in the "pantepuis" of southwestern Venezuela (Fig. 13). Both species are at or near the outer edges of the distribution of the genus. *A. personatus* is the sole atlatpetes in its region; *A. rufinucha* occurs in the general area with *A. fulviceps*, in the latter's northern range, but has been recorded as sympatric with it only at Tilotila (alt. 2,150 m), La Paz, Bolivia. The Tilotila records are those of Buckley, whose collections were made from 900 to 3,700 m (Sclater and Salvin, 1879). The absence of further evidence of sympatry suggests that Buckley's specimens were altitudinally separated, but which were at the higher elevation is unknown because the altitudinal records from elsewhere overlap.

Highly polytypic *A. semirufus* is the species of the Eastern Andes of Colombia and the coastal mountains of Venezuela (Fig. 13). It may be sympatric with *A. albofrenatus* near Bogotá, but the data suggest that *A. semirufus* occurs at higher altitudes.

Presumably *A. personatus* was derived from early *A. semirufus*. Mayr and Phelps (1967), apparently following Chapman (1931), state that *A. personatus* is most closely related to far-distant *A. fulviceps*. However, morphological evidence is inconclusive and derivation of *A. personatus* from *A. semirufus* seems more logical, simply because they are geographically closer.

The long gap between *A. semirufus* of the northern Andes and *A. fulviceps* of the southern Andes is provocative and suggests that the two allospecies are separated by another species or group. The *A. rufinucha* species-group fills the breach without any indication of sympatry, except for the very dubious record of *A. rufinucha simplex* from native "Bogotá" specimens (Fig. 23). This close fit does not seem to be an artifact. *A. fulviceps* superspecies not only is phenotypically similar to the *A. rufinucha* species-group but must also be very closely related and, hence, unable to coexist with it.

Although one could argue well for the inclusion of *A. personatus*, *A. semirufus*, and *A. fulviceps* within the *A. rufinucha* species-

group, there is a morphological cohesiveness among the three species which probably indicates that this group branched from the ancestral stem stock earlier than the individual species making up the *A. rufinucha* species-group.

#### *Atlatpetes citrinellus*

*A. citrinellus*, of Argentina, is the southernmost representative of the genus (Fig. 15). It stands apart from other members of the genus and obviously is an aberrant representative. It does bear some resemblance to *A. fulviceps* without the chestnut crown and cheeks. The two may have had an ancestral branch in common.

#### *Atlatpetes schistaceus* species-group

This group of six closely-related species is distributed through the Andes from western Venezuela to southern Peru (Fig. 24). The species replace one another geographically in a manner reminiscent of the mosaic pattern of the *A. rufinucha* species-group. The group was analyzed earlier (Paynter, 1972) and only brief outlines are given here.

#### *Atlatpetes schistaceus*

This species has the widest distribution of any species within the *A. schistaceus* species-group, ranging disjunctly from the Cordillera de Mérida, Venezuela through the three ranges of the Colombian Andes and thence on the eastern slope to central Ecuador. The species reappears in central eastern Peru and then again in southeastern Peru (Fig. 24). It is mainly a humid temperate region form but does reach the subtropical zone on occasion. Its total range is from 1,850 to 3,750 m. Color and pattern vary geographically; 12 races have been described. It is, therefore, morphologically the most variable of all atlatpetes.

#### *Atlatpetes nationi*

*A. nationi* (Fig. 24) is the southern Andes western slope counterpart of *A. schista-*

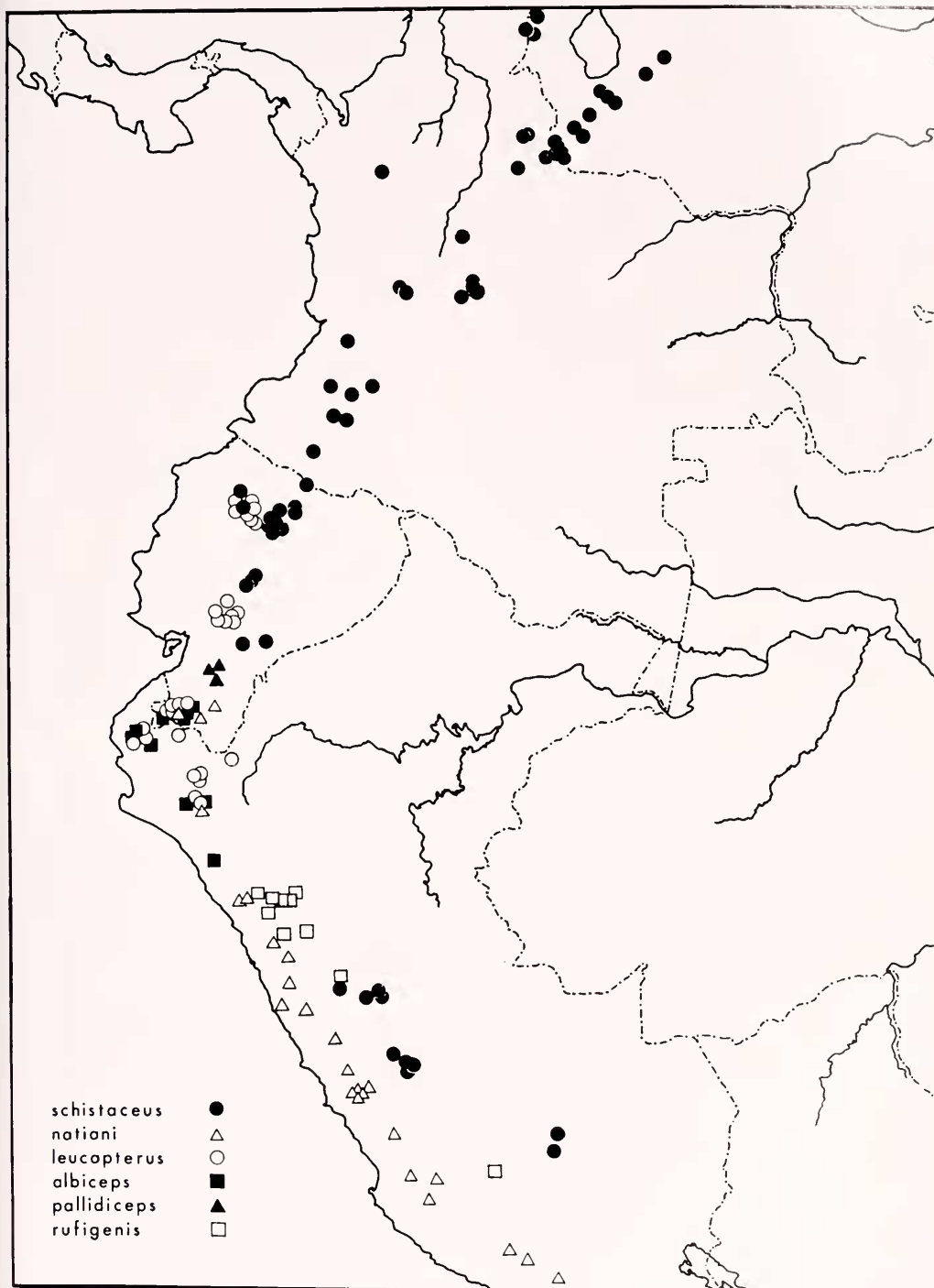


Figure 24. Distribution of the *A. schistaceus* species-group.

*ceus*, occurring from southwestern Ecuador south to Arequipa, Peru, with almost the same altitudinal range as *A. schistaceus* but apparently with a greater tolerance for drier habitats. It is the only *Atlapetes* to range so far south on the western side of the Peruvian Andes. It also has a fragmented distribution and is morphologically varied, with eight races being recognized.

#### *Atlapetes leucopterus*

This, the smallest bird in the genus, is found on the western slopes from northwestern Ecuador to northern Peru, and recently was collected by J. W. Fitzpatrick on the eastern side of the Andes in the Cordillera del Condor, Cajamarca, Peru (Fig. 24). It has a notably wide altitudinal range, having been found from 600 to 2,900 m, and appears to be common in rather xerophytic areas, but it also occurs in moist regions.

Distributional records show three clusters, viz. northern Ecuador, central Ecuador, and southern Ecuador and northwestern Peru (Fig. 24). The northern and central Ecuador populations represent one subspecies and the southern Ecuador and northwestern Peru populations another race. The recently discovered population in brushy edges of cloud forest in the Cordillera del Condor, to the east of the previously known Peruvian range, represents a very distinctive form that has not yet been named.

*A. leucopterus* is sympatric with *A. nationi* and *A. albiceps* in the dry, low mountains of southern Ecuador/northern Peru. These are the only known instances of sympatry within the species-group. The area of sympatry is in a region that probably has been particularly sensitive to variations in climate, owing to its low mountains and proximity to the arid Pacific coast. The vegetation has doubtless varied greatly. The instability would have made the region unsuitable for the long-term presence of any species of *Atlapetes*. The species, now meeting there and overlapping, seem to

have had their origins elsewhere—*nationi*, and probably *albiceps*, to the south and *leucopterus* to the north (see Paynter, 1972: 317–318).

#### *Atlapetes albiceps*

*A. albiceps*, a monotypic taxon, is another western slope form. It is found from southernmost Ecuador to Cajamarca, northern Peru (Fig. 24). It is an arid zone species with an altitudinal range from 250 to 1,500 m.

#### *Atlapetes pallidiceps*

This is another arid area form, ranging from about 1,500 to 2,100 m. It is endemic to the valley of the upper Río Jubones and its tributaries, southwestern Ecuador (Fig. 24).

#### *Atlapetes rufigenis*

*A. rufigenis* is a large species with a population in the drainage system of the Río Marañón, northern Peru and another, racially distinct, population far to the south in the Río Apurimac region (Fig. 24). It occurs from 2,750 to 4,000 m and seems to frequent mesic underbrush.

#### *Atlapetes torquatus* species-group

There are four species within this species-group. The presence of a chestnut pileum in *A. brunneiucha* sharply distinguishes it from *A. torquatus* superspecies, but except for this one character, there is little morphological difference. All four species are surely derived from a common stem. However, because *A. brunneiucha* is frequently sympatric with *A. torquatus*, the two must be old, well-established, species, in contrast to the species comprising the *A. rufinucha* species-group which, because they seem unable to coexist and therefore form a complex geographical mosaic, are presumably actively speciating.

#### *Atlapetes brunneiucha*

*A. brunneiucha* has the most extensive range of any *atlapetes* (Figs. 16, 17) but

shows remarkably few morphological variations, except for the absence of a breast band in the races *apterus*, *allinornatus*, and *inornatus*, three very small populations. This is a notable contrast to the variability within *A. torquatus* superspecies, which is almost as widely distributed.

The lack of morphological variability is probably because *A. brunneinucha* inhabits the interior of moist subtropical forest. This habitat doubtless continued to exist in abundance and with few discontinuities even during the peak of climatic deterioration when lowland forests withdrew to isolated or semi-isolated refugia. Indeed, with the lowering of vegetation zones on the mountains, subtropical forest may have become more abundant than at any period, owing to its presence on the vast shoulders of the mountains.

The morphological differentiation that has occurred in the races *apterus*, *allinornatus*, and *inornatus* is doubtless the result of isolation, but why the breast band is the variable character is unknown. *A. b. apterus* is on an isolated mountain standing in lowland forest in Veracruz; *A. b. allinornatus* is on a northward-projecting spur off the main range of the Venezuelan Andes. There is no geographical feature associated with the range of *A. b. inornatus*, but its origin may be attributed to isolation brought about by climatic changes. Note that the arid coastal belt of western South America reaches northern limits at about the same latitude as the range of *inornatus*. During a warm-dry period the arid zone must have extended higher on the western slopes of the Andes. *A. b. inornatus* may have originated in a surviving pocket of wet, semitropical forest high on these slopes. A refugium in the same area has already been proposed to explain the origin of *A. leucopterus* (Paynter, 1972:317).

#### *Atlapetes torquatus* superspecies

*A. virenticeps*, the northernmost representative of this superspecies (Fig. 18), is a relict population. Its plumage is reminis-

cent of immature *A. torquatus*, but whether this indicates that the plumage of *virenticeps* represents the ancestral pattern of the superspecies, or is a case of reversion from a more "adult" plumage, or is an entirely "new" plumage is unanswerable.

The origin of *A. atricapillus* (Fig. 19) is perhaps one of the most intriguing but baffling problems of this nature in the genus. If, as it seems now, *A. atricapillus* and *A. torquatus* are parapatric, the former is probably a fairly recent offshoot. The fact that it is a lower altitude species than *A. torquatus*, and also occurs mainly in the northern extremities of the Andes suggests that it may have originated on outliers of the main Andean ranges, but more specific speculation is not possible until we have a better knowledge of the range of the species.

The morphological variability of *A. torquatus* (Figs. 19–22) stands in contrast to the uniformity of its sister species *A. brunneinucha*. The difference may lie in their habitats. While both are subtropical forms, although *A. torquatus* also ranges higher, *A. torquatus* is an edge dweller, often frequenting second-growth. Under natural conditions, edges and second-growth are generally uncommon and scattered, which means that populations of *A. torquatus* probably never have been as large or as contiguous as those of *A. brunneinucha*, and presumably this would have resulted in increased polymorphism.

*A. torquatus* seems to be somewhat less restricted to a given biome than many atlapetes, which may be indicative of its nature as a generalist and exploiter of temporary changes in habitats. However, of particular interest is the race *A. t. assimilis* which is strictly a temperate zone form. It is also the only race within the range of the allospecies *A. atricapillus*. This is strongly suggestive of altitudinal displacement, with *A. t. assimilis* moving higher to accommodate *A. a. atricapillus* in the upper tropical zone. However, it should be borne in mind that *assimilis* has an extensive range, only a small part of which is known to be near that



of *A. atricapillus*, and that its restriction to the temperate zone may be for other reasons.

## CONCLUSIONS

The species of *Atlapetes* are most abundant at middle elevations in the northern Andes, and it is assumed that the genus had its origin in that region. This would mean that the genus can be no older than the uppermost Pliocene/lowermost Pleistocene, because this was when the main uplift of the Andes took place (Haffer, 1974: 130). It could, of course, be considerably younger.

The majority of the species seem to have arisen in the northern Andes, but five of the 24 species (*pileatus*, *fulviceps*, *personatus*, *citrinellus*, and *virenticeps*) must have originated well outside of this area and four species (*nationi*, *albiceps*, *rufigenis*, and *pallidiceps*) may have arisen in the mid-portion of the Andes.

The present pattern of distribution, as well as the pattern of speciation, show many indications of having been greatly influenced by climatic changes. The connection between climate and speciation is sometimes seen directly, as when the birds have ranges that coincide with patches of vegetation and the patchiness could only have developed through the disappearance of suitable intervening areas. The fragmentation of belts of vegetation must have been caused by climatic changes. For example, *A. flaviceps* and *A. fuscoolivaceus* seem to have arisen when populations of ancestral *A. tricolor* were stranded in isolated pockets of moist subtropical forest on the eastern slopes of the Central Andes of Colombia, above the arid upper Magdalena valley. Another example may be found in *A. pallidiceps*, a distinctive form isolated in the arid valley of the upper Río Jubones, eastern Ecuador. *A. pallidiceps* is a derivative of *A. leucopterus*, a species of generally wetter areas. In this case the population was left behind by a shrinking belt of moist forest but instead of finding refuge in a

wetter pocket (there are none in the region) adapted to a drier situation.

Other indications of the effect of climatic changes on speciation may be seen in the patterns of distribution. For example, the failure of *A. albinucha gutturalis* of Colombia to diverge appreciably from Central American populations, although well-isolated, while nominate *A. albinucha* of Mexico is markedly different from a series of Central American populations, even though less than 100 kilometers apart (see p. 329), can only be explained by a shifting of biomes through climatic changes. Another illustration is found in the intricate distributional mosaic of the *A. rufinucha* species-group (Fig. 23) which certainly must have arisen through a series of climatic oscillations that caused a series of contractions and expansions in several different populations. There seems no other explanation, for example, for the leap-frog pattern displayed by *A. tricolor* and *A. rufinucha* or for the appearance of populations of *A. albofrenatus* between those of *A. semirufus*.

The 24 species of *Atlapetes* cluster into four main groups which seem to represent four multi-branched evolutionary lines. These pathways and the interrelations of the component species are shown diagrammatically in Figure 25. Starting at the bottom of the diagram and reading clockwise, the following information is indicated.

*A. brunneinucha* and *A. torquatus* (with the three allospecies, *atricapillus*, *torquatus*, and *virenticeps*) share a common origin and form one evolutionary line, the *A. torquatus* species-group. Superspecies *A. albinucha* (with allospecies *albinucha* and *pallidinucha*) is a second main branch. The third, and largest, branch is made up of 12 species. *A. pileatus*, *A. leucopsis*, *A. albofrenatus*, *A. rufinucha* superspecies (with allospecies *rufinucha* and *melanocephalus*), and *A. tricolor* superspecies (with allospecies *flaviceps*, *tricolor*, and *fuscoolivaceus*) form the core of this branch while *A. fulviceps* superspecies (with allospecies *fulviceps*, *semirufus*, and *personatus*) is an off-



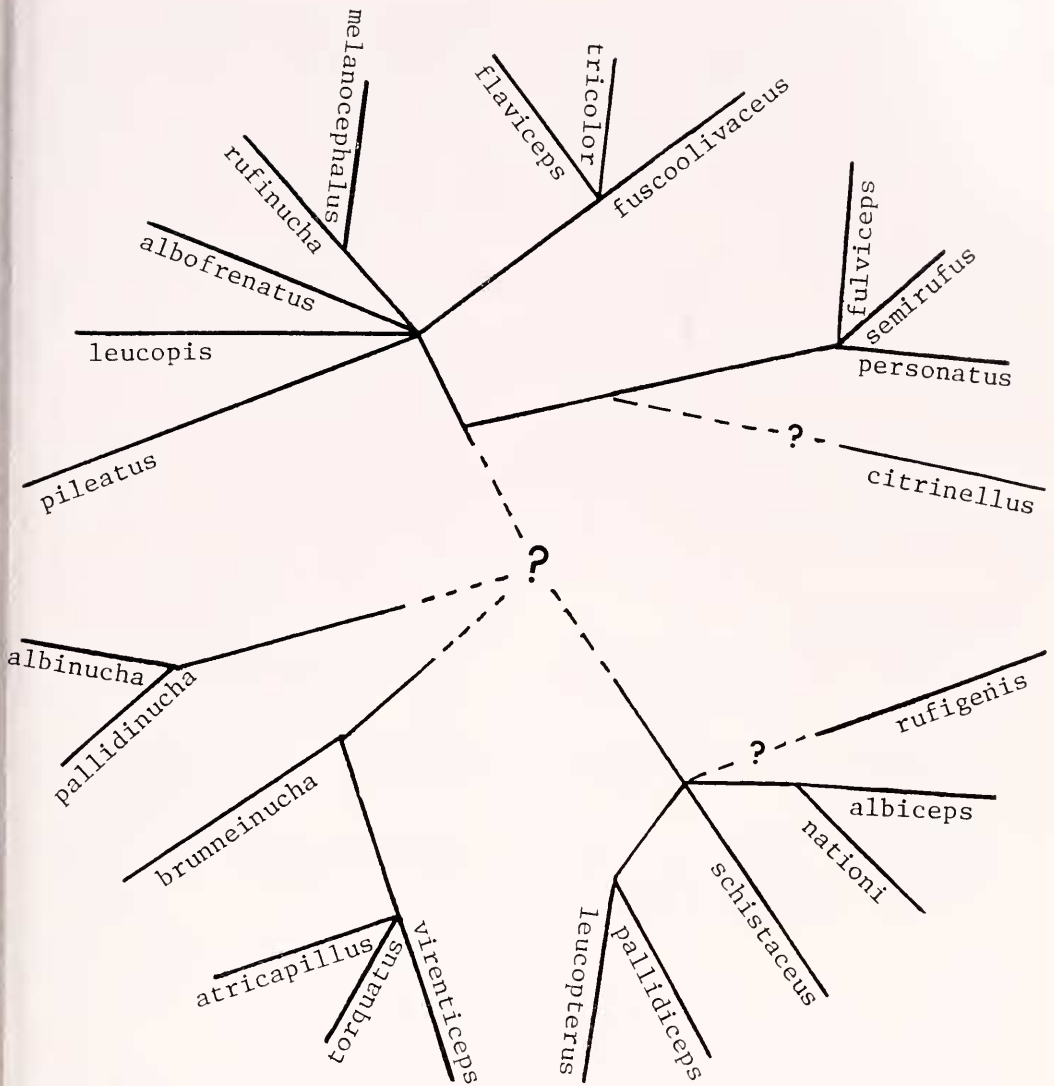


Figure 25. Interrelationships within the four main evolutionary paths in the genus *Atlapetes*. The relative lengths of the lines and their angles are of no significance. See text (p. 366) for details.

shoot of the main branch, and *A. citrinellus* is presumed to be a derivative of this offshoot. The fourth line of descent is the *A. schistaceus* species-group. *A. rufigenis* seems to have been an early offshoot, or it may merely be distinctive because of its distance from the center of the species' distribution. *A. albiceps* and *nationi*, while sharing a common origin from the main

branch, are too distinct to be considered allospecies. *A. schistaceus* seems to represent the main line of evolution for this unit. *A. pallidiceps* and *A. leucopterus* are another pair of species that come off a common point but also are too divergent to be treated as members of a superspecies.

Of particular interest are the *A. rufinucha* species-group and *A. schistaceus* species-

group, which form the two main evolutionary lines within the genus. The former has 11 species (12 if *citrinellus* is included) falling into three superspecies, plus three (or four) separate species, while the *A. schistaceus* species-group is composed of six species, none of which is a member of a superspecies. The species within each species-group are distributed in an intricate checkerboard pattern. Sometimes the species are geographically separated, at other times they are contiguous, and only very rarely are they partially sympatric. In other words, the species within each species-group, even those which are not allopatric, almost invariably do not have overlapping ranges. This general allopatry implies that the species are incompatible and seems to indicate that they have only recently speciated.

#### LITERATURE CITED

- BANGS, O. 1908. Notes on birds from western Colombia. *Proc. Biol. Soc. Washington*, **21**: 157-162.
- BERLIOZ, J. 1932. Nouvelle contribution à l'étude des oiseaux de l'Écuador. *Bull. Mus. Nat. Hist. Nat. Paris*, **4**:620-628.
- BERTONI, A. DE W. 1925. Notas sobre aves del Paraguay, Hornero, **3**:279.
- BLAKE, E. R. 1956. A collection of Panamanian nests and eggs. *Condor*, **58**:386-388.
- . 1958. Birds of Volcán de Chiriquí, Panama. *Fieldiana: Zool.* [Chicago], **36**:499-577.
- CARRIKER, M. A., JR. 1910. An annotated list of the birds of Costa Rica including Cocos Island. *Ann. Carnegie Mus.*, **6**:314-915.
- CHAPMAN, F. M. 1914. Diagnoses of apparently new Colombian birds, II. *Bull. Amer. Mus. Nat. Hist.*, **33**:167-192.
- . 1917. The distribution of bird-life in Colombia. *Bull. Amer. Mus. Nat. Hist.*, **36**: 1-729.
- . 1923a. Mutation among birds in the genus *Buarremon*. *Bull. Amer. Mus. Nat. Hist.*, **48**:243-278.
- . 1923b. Descriptions of proposed new birds from Panama, Venezuela, Ecuador, Peru and Bolivia. *Amer. Mus. Novit.*, No. 67, 12 pp.
- . 1927. Descriptions of new birds from northwestern Peru and western Colombia. *Amer. Mus. Novit.*, No. 250, 7 pp.
- . 1931. The upper zonal bird-life of Mts. Roraima and Duida. *Bull. Amer. Mus. Nat. Hist.*, **63**:1-135.
- CHERRIE, G. K. 1892. A preliminary list of the birds of San José, Costa Rica [part]. *Auk*, **9**: 21-27.
- CODY, M., AND J. H. BROWN. 1970. Character convergence in Mexican finches. *Evolution*, **24**:304-310.
- DE SCHAUENSEE, R. M. 1951. The birds of the Republic of Colombia. *Caldasia*, **5**:873-1112.
- . 1966. *The Species of Birds of South America and their Distribution*. Narbeth, Penna., Livingston Publ. Co., xviii + 577 pp.
- DICKEY, D. R., AND A. J. VAN ROSSEM. 1938. The birds of El Salvador. *Field Mus. Nat. Hist., Zool. Ser.*, **23**:1-609.
- DINELLI, L. 1918. Notas biológicas sobre las aves del noreste de la Rep. Argentina. *Hornero*, **1**:57-68.
- EDWARDS, E. P. 1972. *A Field Guide to the Birds of Mexico*. Sweet Briar, Virginia, E. P. Edwards, 300 pp.
- HAFFER, J. 1974. *Avian Speciation in Tropical South America*. Publ. Nuttall Ornith. Club, No. 14, 390 pp.
- HARDY, J. W., AND T. WEBBER. 1975. A critical list of type specimens of birds in the Moore Laboratory of Zoology at Occidental College. *Contr. Sci., Nat. Hist. Mus., Los Angeles County*, No. 273, 25 pp.
- HELLMAYR, C. E. 1938. Catalogue of birds of the Americas. *Field Mus. Nat. Hist., Zool. Ser.*, **13**(11):vi + 662 pp.
- HILTY, S. L. 1977. *Chlorospingus flavovirens* re-discovered, with notes on other Pacific Colombian and Cauca Valley birds. *Auk*, **94**:44-49.
- LAND, H. C. 1970. *Birds of Guatemala*. Wynnewood, Penna., Livingston Publ. Co., 381 pp.
- MAYR, E., AND W. H. PHELPS, JR. 1967. The origin of the bird fauna of the south Venezuelan highlands. *Bull. Amer. Mus. Nat. Hist.*, **136**:273-327.
- MILLER, A. H. 1960. Additional data on the distribution of some Colombian birds. *Novel. Colombianus*, **1**:235-237.
- . 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. *Univ. Calif. Pubs. Zool.*, **66**:1-78.
- MILLER, A. H., H. FRIEDMANN, L. GRISCOM, AND R. T. MOORE. 1957. Distributional checklist of the birds of Mexico. Part II. *Cooper Ornith. Soc., Pacific Coast Avifauna*, No. 33, 436 pp.
- MOORE, R. T. 1938. New races in the genera of *Vico* and *Buarremon* from Sinaloa. *Proc. Biol. Soc. Washington*, **51**:69-72.
- OLIVARES, A. 1969. *Aves de Cundinamarca*. Univ. Nac. Colombia, Bogotá, 425 pp.

- OLROG, C. C. 1963. Lista y distribución de las aves Argentinas. Univer. Nac. Tucuman, Inst. Miguel Lillo, Opera Lilloana, **9**:1-377.
- PARKES, K. C. 1954. A revision of the Neotropical finch *Atlapetes brunnei-nucha*. Condor, **56**:129-138.
- PAYNTER, R. A., JR. 1957. Birds of Laguna Ocotol. In R. A. Paynter, Jr. (ed.), Biological Investigations in the Selva Lacandona, Chiapas, Mexico. Bull. Mus. Comp. Zool., **116**:249-285.
- . 1964. The type locality of *Atlapetes albinucha*. Auk, **81**:223-224.
- . 1970. Emberizinae, pp. 3-214. In Paynter (ed.), Check-list of Birds of the World. Vol. 13. Cambridge, Mass., Mus. Comparative Zoology, Harvard Univ., xvi + 443 pp.
- . 1972. Biology and evolution of the *Atlapetes schistaceus* species-group (Aves: Emberizinae). Bull. Mus. Comp. Zool., **143**:297-320.
- PAYNTER, R. A., JR., AND M. A. TRAYLOR, JR. 1977. Ornithological Gazetteer of Ecuador. Cambridge, Mass., Mus. Comparative Zoology, Harvard Univ. and Chicago, Ill., Field Mus. Nat. Hist., 151 pp.
- PEREYRA, J. A. 1951. Avifauna Argentina (contribución a la ornitología) [Pt.]. Hornero, **9**:291-347.
- PETERSON, R. T., AND E. L. CHALIF. 1973. A Field Guide to Mexican Birds. Boston, Houghton Mifflin, 298 pp.
- PHELPS, W. H., AND W. H. PHELPS, JR. 1963. Lista de las aves de Venezuela on su distribución. Bol. Soc. Venezolana Cienc. Nat., **24**:1-479.
- PHILLIPS, A. 1966. Further systematic notes on Mexican birds. Bull. Brit. Ornith. Club, **86**:86-94, 103-112, 125-131, 148-159.
- RIDGELEY, R. 1976. A Guide to the Birds of Panama. Princeton Univ. Press, 394 pp.
- ROWLEY, J. S. 1968. Geographic variation in four species of birds. Occas. Papers, Western Found. Vert. Zool. [Los Angeles], No. 1, 10 pp.
- SCHÄFER, E., AND W. H. PHELPS. 1954. Aves de Rancho Grande. Bol. Soc. Venezolana Cienc. Nat., **16**:3-167.
- SCHALDACH, W. J., JR. 1963. The avifauna of Colima and adjacent Jalisco. Proc. Western Found. Vert. Zool., **1**:1-100.
- SCLATER, P. L., AND O. SALVIN. 1879. On the birds collected in Bolivia by Mr. C. Buckley. Proc. Zool. Soc. London, 1879:588-645.
- SKUTCH, A. F. 1954. Life Histories of Central American Birds. Cooper Ornith. Soc., Pacific Coast Avifauna, No. 31, 448 pp.
- . 1967. Life Histories of Central American Highland Birds. Publ. Nuttall Ornith. Club, No. 7, 213 pp.
- SLUD, P. 1964. The birds of Costa Rica. Bull. Amer. Mus. Nat. Hist., **128**:1-430.
- SMYTH, C. H. 1928. Description de una colección de huevos de aves Argentinas [Pt. 2]. Hornero, **4**:125-152.
- TACZANOWSKI, L. 1884. Ornithologie du Pérou. Vol. 2. A. Rennes, 566 pp.
- TODD, W. E. C., AND M. A. CARRIKER, JR. 1922. The birds of the Santa Marta region of Colombia: a study in altitudinal distribution. Ann. Carnegie Mus., **14**:1-611.
- WETMORE, A. 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. Bull. U.S. Natl. Mus., **133**:1-448.